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The automatic pilot: Cognitive, attentional and neurological aspects of the online correction of manual aiming movements.

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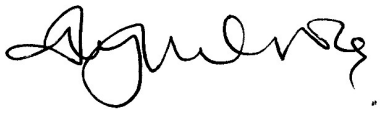
Declaration

I hereby declare that this thesis is of my own composition, and that it contains no material previously submitted for the award of any other degree. The work reported in this thesis has been executed by myself, except where due acknowledgement is made in the text.



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Previous published dissemination

The findings from Chapter Two have been presented via a poster, and have since been published:

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The findings from Chapter Four have also been published:

McIntosh, R.D., Mulroue, A., Blangero, A., Pisella, L. & Rossetti, Y. (2011). Correlated deficits of perception and action in optic ataxia. *Neuropsychologia, 49,* 131-137.

Abstract

When the target of a reaching movement is displaced suddenly, people update their movement to take account of the jump, correcting their trajectory online to end the movement at the new target location. These corrections are initiated too rapidly to be conscious, and occur when they are uninstructed (Pisella et al., 2000) or the participant is unaware of the change in location (Goodale et al., 1986). These findings have been taken as evidence that fast corrections occur automatically, and the spatial updating of reach trajectories has become known as the 'automatic pilot' (Pisella et al., 2000). This thesis set out to investigate the cognitive, attentional and neurological aspects of the automatic pilot, in three series of related experiments, all employing a double-step reaching task.

Experiments 1 - 4 investigated how strongly automatic reach corrections are, by manipulating the influence of conscious intention and cognitive load. These experiments confirmed that the automatic pilot is at most *weakly* automatic, as correction efficiency is enhanced by an explicit instruction to follow target jumps and, conversely, corrections can be overridden by an intention to resist them. However, voluntary inhibition of the automatic pilot can be disrupted by placing participants under heavy cognitive load, whilst voluntary enhancement is unaffected by this manipulation. Thus, voluntary suppression of the automatic pilot is effortful, but enhancement towards greater responsiveness is seemingly effortless.

Experiments 5 - 8 explored the properties of the visual target displacement that drive the automatic pilot response in a double-step reaching task. These

experiments demonstrate that correction efficiency is lawfully related to jump salience, but that the onset of the new target location drives correction responses more powerfully than the offset of the original target. However, the maximal correction rates obtained from a simultaneous onset and offset, were too great to be attributed simply to the additive influences of onsets and offsets. The onset and offset components of the target jump are thus synergistic. It is suggested that this reflects the contribution of an apparent motion signal induced by simultaneous onset and offsets, which strongly drives the automatic pilot system.

Experiment 9 examined an asymmetry in correction efficiency, favouring rightward over leftward target jumps, evident throughout the earlier experiments. Correction efficiency was assessed for right- and left-handed participants responding to rightward and leftward target jumps. The pattern of results indicated that each hand is advantaged for responding to ipsilaterally-directed jumps, which may reflect biomechanical or hemispheric compatibility effects. However, there was also an overall differential advantage for rightward jumps, which was independent of handedness, or hand used. This suggests a left-hemispheric advantage for automatic correction behaviour, independent of handedness. Finally, Experiments 10 - 14 considered whether the automatic pilot deficit in optic ataxia is simply a manifestation of the more general misreaching deficit. Across several different target conditions, the pattern of online correction in optic ataxia refuted a simple misreaching explanation, suggesting that it is a specific functional consequence of dorsal stream damage.

Contents

Chapter One:

Introduction

The automatic pilot of the hand

When we reach towards an object, our initial aim may be imperfect, or environmental changes, such as movements of the target or of the body, may perturb our movement. Provided that these errors or perturbations are relatively minor, we compensate for them without effort. Indeed, we typically acquire our target with no awareness of the fine adjustments that we have made during the course of our reach (see below for a discussion of the relation of online correction to awareness). The experimental study of this ability is usually traced to Woodworth (1899), who divided a reaching action conceptually into an initial ballistic phase, in which a predefined motor command is executed in a feedforward manner, and a later controlled phase, in which sensory feedback from the movement is used to correct for errors in the ballistic movement and home in upon the target. The second, feedback-based form of control was assumed to be important mainly in the late decelerating portion of a reach for two reasons. First, sensory reafference takes time (at least 80-100 ms, according to work reviewed by Paillard, 1996), so feedback information is unavailable until the initial part of the movement has been completed. Second, because of the sensory delay, afferent feedback is always out-of-date, lagging behind the real state of the world by 80-100 ms. Feedback-based control is likely to be more useful during the late, low-velocity portion of the reach, during which the hand position will change less dramatically during the sensory delay, and during which the proximity of the hand to the target makes the required corrections easier to compute.

The ability for online correction in reaching is studied experimentally by artificially introducing spatial errors during a movement, and studying the motor system's corrective response. Errors can be introduced in a variety of ways, for instance by applying a force to the moving arm, knocking it off course (e.g. Wolpert, Gharamani, & Jordan, 1995), or by perturbing vision of the target, for instance by using optically-displacing prisms, so that the initial movement is inaccurate (e.g. Jakobson & Goodale, 1989). However, by far the simplest, and correspondingly the most popular method is to generate an aiming error simply by changing the position of the target during the course of the reach. This general paradigm, drawn from the study of saccadic eye movements, is known as a double-step task, referring to the two stages of target presentation. Firstly the target is presented in an initial location (T1), and then secondly, the target is presented in a new perturbed location (T2). The simultaneous removal and appearance of the target between the two locations creates the illusion of the target jumping from one location to the other.

Despite the complex processes involved in changing the programmed course of the movement, the motor system is able to respond to the target jump in double step reaching tasks within about 100ms (Soechting & Lacquaniti, 1983; Prablanc & Martin, 1992, Brenner & Smeets, 1997). The adjustments to the hand's trajectory typically blend into the ongoing movement, so that the hand's trajectory deviates smoothly towards the new location without additional movement time cost or changes in the velocity profile (for example, a secondary peak), and without the need to interrupt and reprogram the movement (Georgopoulos, Kalaska & Massey, 1981; Soechting & Lacquaniti, 1983; Goodale, Pélisson, Prablanc, 1986; Prablanc & Martin, 1992). Within the literature, this specific behavioural function has come to be known as 'the automatic pilot of the hand' (Pisella, Gréa, Tilikete, Desmurget, Rode, Boisson & Rossetti, 2000).

In many naturalistic tasks, of course, the hand does not act alone, but rather is coordinated closely with movements of the eyes that influence the available visual information. Typically, we look at the object that we are reaching, and it is

the eyes that move first, then the head and then the hand. It was initially thought that this ordered sequence was required to capture the target in foveal vision in order to program the reaching movement, with as accurate information as possible (Goodale & Murphy, 1997). Biguer et al.(1982, as cited in Desmurget & Grafton, 2000) however, have demonstrated that eye, head and hand movements are initiated in parallel and the delay between the eye and the hand movement is simply due to inertia, with the hand taking longer to start moving. This suggests that the motor program is actually planned using imperfect peripheral information and so would be likely to benefit from feedback from early on in the movement, rather than just towards the end of the movement (Woodworth, 1899; Desmurget & Grafton, 2000). Working in parallel also reduces the time required to achieve the goal; it would be inefficient for the motor system to have to await foveation before it can act (Pélisson, Prablanc, Goodale, & Jeannerod, 1986).

Although the system doesn't have to wait for foveation, the first saccade made towards a target is usually completed before the hand has started to move. A common behaviour of the oculomotor system is that the initial saccade tends to undershoot the target and then it is followed by a second corrective saccade that brings the target onto the fovea (Henson, 1978). Pélisson et al. (1986) made use of this oculomotor habit and perturbed the target in a reaching movement during the first saccade, at the point of maximum velocity, in order to displace the target during saccadic suppression, and therefore eliminate conscious awareness of the change. The retinal error following the first saccade is then computed to update the information on target position, which is immediately available to adjust the trajectory of the hand (Goodale et al., 1986; Pélissonet al., 1986). By altering the target position during the saccade, Pélisson et al. (1986) were able to demonstrate that people are able to update their movements to a perturbation, even if they were not consciously aware of the change in the target position (see also Goodale et al., 1986). It is important to note that these experiments were considered to closely model the natural situation of looking

and reaching, in which the retinal error at the end of the initial saccade is used to adjust the initial reaching movement, maximising reach accuracy. The fact that participants could correct for the artificially-induced reaching errors without additional movement time, with no evidence of reprogramming movements post perturbation, indicates that this method successfully models the natural situation (Pélisson et al., 1986; Prablanc & Martin, 1992).

A further important aspect of Goodale et al.'s (1986) findings was that these rapid online corrections were obtained even when there was no visual feedback from the hand during the reaching movement, indicating that kinaesthetic feedback may also be used to estimate current arm position during reaching. An even more surprising finding, however, was that such corrections could still occur (albeit less accurately) in the absence of visual feedback in a patient with complete peripheral deafferentation due to sensory polyneuropathy, who therefore also had no kinaesthetic feedback available (Bard, Hay, & Fleury, 1999). This result establishes that the comparison of hand position with target position is not based solely upon sensory feedback, but may also include an 'internal feedback' loop, whereby a copy of the efferent motor command is used as the basis for predicting the sensory consequences of the movement, in terms of the hand's likely future position. Crucially, this forward modelling may allow the motor system to overcome the delays inherent in sensory reafference, because corrections can be made based upon the detection of error in a comparison of the hand's predicted future position in relation to the target, and therefore for online correction to be implemented continuously throughout the course of the movement (Wolpert et al., 1995). The incorporation of forward modelling based on efferent copy of motor commands is the most crucial modification distinguishing contemporary models of feedforward and feedback motor control from Woodworth's (1899) classical two-phase account (see Desmurget & Grafton, 2000, for a review).

The automatic pilot and automaticity

The studies discussed above demonstrate the highly skilled ability of the motor system to accurately adjust movements without conscious awareness of the target jump. This ability is thought to depend critically upon dorsal stream structures in the superior parietal lobe, being perhaps the clearest behavioural instance of vision-for-action, as proposed by Milner and Goodale (1995). Strong evidence for this view came initially from the study of patient IG, who had optic ataxia following bilateral dorsal stream lesions. Unlike normal participants, IG was found to make no fast online corrections in a double-step reaching task, instead ending up at the original target location, unless she made temporally extended movements of 400 ms or more (Pisella et al., 2000). This basic observation was subsequently confirmed for IG in a reach-to-grasp task (Gréa, Pisella, Rossetti, Desmurget, Tilikete, Grafton, Prablanc, & Vighetto, 2002), and replicated in another patient (CF) with optic ataxia (Blangero et al., 2008). Moreover, Desmurget, Epstein, Turner, Prablanc, Alexander, and Grafton, (1999) were able to induce an online control deficit for normal participants reaching with the right hand, by applying single-pulse TMS to the left superior parietal lobe at the moment of the target jump.

If the dorsal stream is responsible for the fast online correction of reaching, and the dorsal stream is an unconscious guidance system that operates without visual awareness (Milner & Goodale, 1995), then we should expect to observe clear evidence of dissociations of online correction ability from awareness. Clearly, the results of Pélisson et al. (1986; also Goodale et al., 1986) are consistent with this prediction, since participants were shown to make trajectory corrections to compensate for a target jump applied under saccadic suppression, yet be at chance in guessing whether or not the target had moved on a given trial. Castiello and colleagues (Castiello, Paulignan & Jeannerod, 1991; Castiello & Jeannerod, 1991) provide converging evidence for unconscious operation of the automatic pilot, having investigated the time lag

between the initiation of a motor correction and the conscious perception of the target jump that triggered it. Participants were instructed to perform manual grasping movements in a double-step task and to verbally express any awareness of the target jump by saying Tah! (a vocal utterance unrelated to the nature of the stimulus). Grasping tasks are more complex than the pointing or reaching tasks typically employed in the investigation of online control. Grasping movements are made up of two phases: a transport or reaching phase, which involves the hand moving towards the object to be grasped, and a grasping phase, in which the fingers and thumb move and shape to grasp the object. Due to this complexity, Castiello and colleagues (Castiello, Paulignan & Jeannerod, 1991; Castiello & Jeannerod, 1991) only report the results from the transport component of the movement. The task required participants to grasp one of three translucent dowels, which was illuminated to identify the target object. The location perturbation was achieved by switching the illumination of one of the rods to another rod to the left or the right of the original target object.

In line with other reports, the minimum amount of time required for the hand to react to the shift in target position was 100-110ms (with movement times for the total movement duration for unperturbed and perturbed trials being 611ms and 735 ms respectively). The main measures of interest for Castiello and colleagues were the reaction times to the stimulus onset and the perturbation. Motor and vocal reaction times were measured as the delay between the illumination of the target and the onset of the movement, or the onset of the vocal response. These were compared to the vocal reaction time to the perturbation of the target, which was measured as the delay between the release of the start switch (which triggered the perturbation) and the onset of the second response. Participants therefore had to produce two vocalisations during a perturbed trial, one to indicate perception of the target and the second to signal the change in the targets location or size. The timing of the motor response in the perturbed trials was defined by the point of increase in lateral acceleration in the direction of the target perturbation. Reasonable correlations

were found between the first vocal reaction time and the motor reaction time (control trials r=0.57, perturbed right trials r=0.66, perturbed left r=0.75), but there was no relationship between the movement kinematics and the timing of the second vocal reaction time in response to the noticed perturbation. The perturbation was triggered at movement onset, yet it took over 400ms to vocalise the conscious perception of the perturbation, either in target location (Castiello et al., 1991), or the target size (Castiello & Jeannerod, 1991), with a difference of 315 ms on average between the motor and perceptual reaction times. A series of control tasks demonstrated that the motor and vocal responses are produced independently: the kinematics of the reaching movements were not affected by the production of the vocal response and the ability to make a vocal response was not affected by performing the motor task (Castiello et al., 1991; Castiello & Jeannerod, 1991). Castiello and colleagues argue that the delay between the manual correction and the vocal response is due to the processing lag between action and awareness, not due to the additional time required to produce a vocal response.

The above studies by Castiello and colleagues (Castiello et al., 1991; Castiello & Jeannerod, 1991) demonstrate that the processing required to generate perceptual awareness is slower than the production of visuomotor responses; and the verbal response requires visual awareness in order to be generated and the manual movement does not. The relationship between action and awareness however, is not fully unpicked in these studies. Johnson and Haggard (2005) suggest that motor performance and perceptual awareness are confounded, and that there is a need to distinguish between motor and perceptual representations and distinguish between the conscious and unconscious processes involved. Their chosen methodology was to make participants reproduce the spatial aspects of their reaching movement immediately after each trial, as well as also adopting the 'Tah!' verbal response (Castiello et al., 1991; Castiello & Jeannerod, 1991), in an attempt to differentiate between motor performance, motor awareness and perceptual

awareness (Johnson, van Beers, & Haggard, 2002; Johnson & Haggard, 2005). Johnson & Haggard (2005) compared the spatial parameters of standard pointing movements in a double-step task, by asking participants to produce a reproduction of the movement immediately after the trial, using the relationship between the real and reproduced end points as a measure of motor awareness. Participants were able to accurately reproduce the spatial characteristics of their pointing movements, even when they did not report seeing the target shift. So although they were perceptually unaware of the target shift, they were still aware that their movement had contained a deviation and reproduced the deviation in the correct direction (Johnson & Haggard, 2005). Johnson & Haggard (2005) conclude that the visual information to guide motor movements and the visual information available for perceptual awareness dissociate. In the studies by Johnson and colleagues (Johnson et al., 2002; Johnson & Haggard, 2005), there was a replication of previous findings, with no perceptual awareness needed for manual corrections to be produced. These findings, and others to be reviewed in the next chapter, support the designation of the automatic pilot system as, at least to some degree, autonomous from conscious awareness.

This autonomy could be suggestive of an automatic process. Automaticity can be considered as a feature of a process that emerges when several processing characteristics are combined (Palmer & Jonides, 1988). Two particular features which tend to co-occur when a process is deemed automatic are insensitivity to concurrent load and insensitivity to voluntary control (Yantis & Jonides, 1990). The implications of these features for the automatic pilot would be that correction behaviour would be stimulus driven regardless of the cognitive goal.

These features are also criteria for Fodor's (1983) classification of modularity. In addition to the insensitivity to central cognitive goals, the automatic pilot system would need to be domain-specific, innately specified, hardwired, autonomous, and informationally encapsulated to be classed as a modular

system. Several of the experiments reported in this thesis may help to clarify whether the automatic pilot system can be considered as modular. The literature supports that the dorsal stream computes a constrained class of specific inputs bottom-up, focusing on entities relevant only to its particular processing capacities, and also it appears to be associated with specific, localised neural structure. There is an assumption in the literature that the system is automatic and thus stimulus driven and insensitive to central cognitive goals, which is explored in Chapters 2 and 3. On the other hand, the information from the dorsal and ventral visual systems are integrated to provide a unitary experience (Goodale & Milner, 1992), practice and learning have an influence on correction behaviour, and the mandatory nature of the correction response can be questioned (Chapter 2), which do not fit with the modularity model. The concept of automaticity will be discussed further in the following chapter.

The present thesis

Having provided a brief introductory framework for the empirical portion of this thesis, this chapter will close with a brief overview of the three chapters to follow, in which these experiments are reported. Detailed reviews of the literature relevant to these studies will be given in the introductions to the relevant chapters, in order to respect the thematic of material within this thesis. The overall topic of study is the automatic pilot of the hand, as studied using double-step reaching tasks, and each thesis chapter will consider a different aspect of automatic pilot function, presenting a series of linked studies addressing this topic. Experiments 1-4 (Chapter 2) are commonly concerned with 'cognitive aspects of the automatic pilot', specifically investigating the level of automaticity that we should ascribe to this behavioural category, and the degree to which functioning is modifiable by top-down factors. Experiments 5-8 (Chapter 3) are concerned with 'attentional aspects of the automatic pilot',

specifically those visual stimulus parameters that affect the responsiveness of online correction in a standard double step task (with the jump made in free vision). Experiments 9-14 are concerned with 'neurological aspects of the automatic pilot', investigating first possible hemispheric asymmetries of its function in left- and right-handers reaching with either hand, then turning to the consequences of dorsal stream lesions for online correction in four patients with optic ataxia, each considered as a single case. Each empirical chapter will round off with a discussion of results in relation to the relevant literature. Finally, the thesis will round off with a brief general overview and discussion of the empirical contribution represented by this work.

Chapter Two:

Cognitive aspects of the automatic pilot

Fast in-flight correction of reaching movements is a response that occurs even without instruction (Day & Lyon, 2000; Pisella et al, 2000), and which can be pre-conscious (e.g. Castiello et al, 1991; Goodale et al, 1986). The fact that the corrective system can bypass conscious perception has been used as evidence to suggest that the fast corrections made during a pointing or reaching movement towards a perturbed target are produced in a highly automatic fashion, through the dorsal stream. Although the unconscious execution of a correction implies that the behaviour is automatic, the level of this automaticity has not been well defined. There are two criteria that have emerged from the literature that jointly need to be met for a process to be classed as highly or strongly automatic (Palmer & Jonides, 1988). The first criterion is the intentionality criterion, which asserts that the process must not be able to be overridden or stopped by the person's intentions. The second criterion is the concurrent load criterion, which states that a concurrent cognitive or perceptual load should not disrupt processing efficiency. These criteria have not been fully addressed in reference to the online corrections produced towards a target perturbation. The term 'automatic pilot' was applied to this ability by Pisella and colleagues (Pisella et al., 2000) after unexpected findings from a study revealed that corrections occur when they are not part of the task goal for the participant; making corrections unintentionally however, is very different to corrections occurring when the participant intentionally sets out not to make them, and it would be the latter

ability which would need to be demonstrated in order to fulfil the intentionality criterion.

Pisella et al. (2000) employed a 'STOP' response, which required participants to abort their movement when they perceived the perturbation, as well as instructing participants in a 'GO' condition to follow the target perturbation. The target perturbation was either signalled by a change in target location or by a colour change. In the location condition, one target was extinguished as another was presented to make the target appear to jump. In the colour condition, one red and one green circle were both visible and in a perturbation trial, the red and green circles swapped places. The targets were presented on a touchscreen, and participants were required to reach from the start position at the centre of the bottom of the screen to one of two target positions at the centre of the top of the screen. Using both the location and the colour conditions, Pisella et al. (2000) explored whether the ongoing pointing movement could be corrected (GO instruction) or interrupted (STOP instruction) in an attempt to pit the 'automatic' correction response up against the intentional STOP response. Participants were required to complete the conditions under a series of different movement times (200, 250, 300, and 350ms), with movement time and final endpoint position recorded for analysis.

Corrections were made in the location-GO condition for all movement times. Pisella et al. (2000) hypothesised that compliance with the STOP instruction would result in participants successfully interrupting their movement, and failure to comply would result in landing on the screen in the location of T1. In contrast to their prediction, a significant percentage of corrective movements occurred in the direction of the target jump despite the STOP instruction, in the location condition for movement times between 200 and 300ms. After touching the screen in the location of T2, the participants were frustrated and aware of the mistake they had made, which Pisella et al. (2000) took as evidence of 'irrepressible motor corrections' (Pisella et al., 2000; pg.730) being driven

towards the new target location. It appears that the location information is processed during the movement execution and is able to distract the hand away from the intentional instruction and the initial programmed trajectory. The similar timings between the corrections under the GO and the STOP instructions suggest that these early corrections result from the same guidance system, which is independent of instructions and therefore automatic. In contrast, there were no automatic corrections in the colour-STOP group. Corrections were produced towards the new target location in the colour-STOP condition, but these occurred at much longer movement times, indicating that only intentional corrections could be made based on the colour cue, leaving Pisella et al. (2000) to conclude that 'the visuomotor transformations of the hand's 'automatic pilot' may be specific to location processing' (Pisella et al., 2000; pg. 731).

The presence of corrections in the Pisella et al.'s (2000) study was established by using the endpoints of the movements, however in order to fully understand the online control of a movement, it is necessary to be able to examine the spatial and temporal aspects of the trajectory (Day and Lyon, 2000; Cressman Franks, Enns, & Chua, 2006). The advantage of recording the kinematic elements of the movement is that it results in many more data points, as every time point of the movement can be sampled, producing a more powerful analysis. It also allows for a more detailed understanding of hand's trajectory, by identifying when corrections first occur and removing the need for the movement to be completed for it to be classed as corrected or otherwise.

In a follow up to Pisella et al.'s (2000) study, Cressman et al. (2006) addressed the kinematics of the hand's trajectory under GO and STOP instructions to both colour and location perturbations. Importantly, Cressman et al. (2006) also reported the colour-GO results, to provide a baseline for the speed and accuracy of detecting colour changes. The key question in the Cressman et al. (2006) study was whether colour change detection is less efficient than location change detection. They found more corrections towards the new target location in the

GO than in the STOP condition and also more corrections in the location condition than the colour condition, with corrections to colour taking up to 40ms longer, in comparison with the location perturbations. Location and colour are not processed with equal efficiency (Cressman et al., 2006). Target perturbations cued by colour are much less efficient than target perturbations cued by location change, resulting in a reduced number of corrections, a reduced number of successfully stopped trials, longer movement times and an increased latency for correction, as colour information is not detected as early as location information. These findings support Pisella et al.'s (2000) conclusion that automatic modifications are elicited by changes in target location, and not changes in location signalled by colour. In additional support, the Cressman et al. (2006) study also measured higher rates of corrected trajectories in the perturbed trials, than the rates reported by Pisella et al. (2000), suggesting that Pisella et al.'s (2000) methods of analysis may have underestimated the number of corrected movements because of the inability to include successfully stopped trials in the endpoint analysis.

The results from the STOP response provides evidence that the automatic pilot is at least weakly automatic, as the hand either ends up in a corrected position before the movement is aborted, or ends up touching the new target location despite this being uninstructed. This behaviour is observed even though the participants are instructed to pull their hand back or stop the movement at the onset of the target jump, and it is understood by Pisella et al. (2000) to demonstrate that the correction system can take priority over voluntary motor control system, and can impede upon the goal-behaviour of the participant. If the intention to stop can be dominated by the automatic pilot, what about an intention to move in the opposite direction? In a modification of an established paradigm from the eye movement literature, the anti-point task uses the same instructions as the anti-saccade task (Hallett, 1978). The anti-saccade task is an informative task for investigating the influence of cognitive control on reflexive, automatic responses. The task requires participants to suppress the automatic

urge to look at a target abruptly onset in the peripheral visual field and to consciously look to a location in the opposite direction to the target presentation. The important aspect in this task is the top-down inhibition of the highly reflexive saccade response, and researchers have applied a modified version of the anti-saccade task to the question of automaticity in the automatic pilot for the hand.

A target is presented centrally on a screen and on one third of trials is then perturbed to a location on the left or the right, 25ms after the initiation of the pointing movement. In the anti-point trials, the participant is required to point to a location in the opposite direction to the target presentation (Day & Lyon, 2000; Johnson et al., 2002). These tasks have demonstrated that movements intentionally aimed away from the target, initially deviate towards the new target location, and hence away from the participants' intentions. In the Day and Lyon (2000) task, the early corrections in the direction of the target jump occurred at around 125ms in both the reach towards and the reach opposite conditions, with a secondary movement in the reach opposite trajectory at around 200ms. These initial corrections occurred without conscious intention, suggesting that they are highly automatic (Johnson et al., 2002), yet Day and Lyon (2000) noticed that the pull towards the target was less strong in trials when the intention was to move in the opposite direction, suggesting a 'limited amount of voluntary modification' (Day & Lyon, 2000; pg. 166), and indicating a top-down influence that would question strong automaticity. Further to this, the secondary part of the movement, away from the target direction could be classed as a voluntary response, as it was modifiable by the participants' intentions, yet this modification occurred at around 200ms. Day and Lyon (2000) argue that for it to be classed as a truly voluntary response, the participant would need to be consciously aware to initiate the response, and as discussed earlier, the studies by Castiello and colleagues (Castiello et al., 1991; Castiello & Jeannerod, 1991) suggest it takes 400ms to signal awareness. To account for these discrepancies in the evidence for a highly automatic automatic

pilot, Day and Lyon (2000) suggest that motor responses occupy a spectrum of automaticity, from least to most automatic (Hughlings Jackson, 1958), or from least to most modifiable. In regard to the secondary responses in the anti-point task, Day and Lyon (2000) class them as at the least automatic end, with the early responses nearer the most automatic end of the automatic spectrum.

As discussed, for a behaviour or process to be classed as highly automatic, the behaviour needs to be produced despite voluntary intention and be insensitive to concurrent cognitive load. These two criteria will be explored in turn in the current chapter, firstly by requiring participants to suppress corrections towards a perturbed target location, and secondly, to perform a double-step reaching task under dual task conditions.

The STOP findings from the Pisella et al. (2000) study have since been incorrectly understood as evidence of corrections occurring against the participant's intentions, rather than being a result of nonspecific instructions, for example:

'…Based on their findings, Pisella et al. (2000) characterised the PPC as an online control 'automatic pilot', a system that can update rapid movements even when there is no conscious intention to do so – **even in fact when there is a conscious intention *not* to do so**' (Cameron, Franks, Enns & Chua, 2007: p. 298, emphasis added).

These uninstructed STOP corrections do add weight to the automaticity debate, but the nature of the task instruction given to the participant does not fulfil the intentionality criterion for these corrections to be classed as automatic. The anti-point tasks appear to go a step closer to investigate the influence of intention on pointing behaviour, yet both the STOP and the anti-pointing response are essentially the same, in that they are late, delayed, conscious mechanisms that take time to be initiated under voluntary control. In order to

fully explore whether corrections still occur towards a target location perturbation can be voluntarily suppressed, it is necessary to explicitly instruct the participant not to make them. The participants in Experiment 1 will be instructed to point to the target and to continue to point to the original location of the target if the target is perturbed, thereby directly testing whether online corrections satisfy the intentionality criterion for strong automaticity.

Hypotheses

Experiment 1 will investigate the automaticity of movement corrections in manual aiming movements. The established GO and STOP instructions will be employed, as will a new NOGO instruction, in which participants will be required to point at the original location of the dot on all trials. Previous studies have shown that participants will correct to the new target location when not instructed to do so (Pisella et al., 2000; Cressman et al., 2006), suggesting that the automatic pilot is at least weakly automatic, but Experiment 1 investigates what happens when participants are explicitly instructed *not* to do so. If the automatic pilot is highly automatic, then participants will be unable to follow task instructions to point to the original location of the dot, and will be drawn to the new target location. If participants are able to complete the task successfully then the strong automaticity of these corrections can be called into question.

Experiment 1: Methods

Participants

Twenty-four naïve adult volunteers (17 females and 7 males, mean age: 27.53 years) took part in the study. The majority of these volunteers were recruited

amongst the Postgraduate students in the Psychology Department at the University of Edinburgh. All of the participants were right-handed and reported no visual or motor deficits and were allocated, in rotating order, to one of three groups.

Design

The study consisted of three between-subject conditions, the GO condition, the STOP condition and the NOGO condition. Each condition was made of two blocks of 100 trials, with 20 practice trials before the first block and 10 practice trials given before the start of the second block. Each condition had a 20% perturbation rate, with the target jumping to the left or right an equal number of times, replicating aspects of Pisella et al. (2000). On the further 80% of trials, the target remained stationary when the participant released the button. Across all trials, the target was presented on the right in 50% of trials and on the left in the other 50% of trials. All stimuli were presented in a random order and a break was given to the participant between blocks. At the end of the second block, eight calibration trials were recorded, with the index finger positioned on the response button, the centre of the screen, 27mm to the left and 27mm to the right of the centre, to provide reference points for the calculation of spatial errors.

Apparatus

The participant sat at a desk with their left hand resting on their lap and their right-hand index finger resting on the start button. Stimuli were presented on a 3M M170 5-wire resistive touch-screen (active display area 340 x 270mm, resolution 1024 x 768 pixels) in front of the participant, approximately 370 mm from the response button (with a distance of 505mm from centre of screen to the start button) in a dimly illuminated room. The stimulus was a white dot, 10mm in diameter, presented on a black background to reduce glare. On all

trials, the target appeared 27mm to the left or 27mm to the right of the centre of the screen when the button was pressed, and either stayed in its initial position (unperturbed trials) or made a jump to 27 mm to the left or right of the central position in the perturbation trials, when the button was released. The target dot was presented when the start button was depressed, and remained on screen for 350ms from the initiation of the movement.

Infrared tracking equipment (Optotrak: Northern Digital Inc., Waterloo, Ontario, Canada) was used to record the kinematic features of the aiming movement from commencement to cessation at 200Hz for the duration of 1 second. One infrared diode was secured to the participants' right index finger.

Two tones were used to pace the participant's movements. The first tone was sounded 350ms after movement commencement and participants were instructed to touch the dot on the screen in time with the beep. At this time, the target dot was removed from the screen. The second tone was sounded 1000ms after the start of the movement and participants were instructed to return to the start button after hearing the second beep.

Procedure

The participants were told that when they pushed down on the response button, a dot would appear on the screen. The participants were told that their job was to touch the dot on the screen and hold their finger there until they heard the second beep. They should then bring their finger back to the button and press down to initiate the next trial. The further instructions differed for each condition:

GO condition: The participants were told that in some of the trials the dot would jump to another location on the screen and that their job was to follow the dot and touch the dot wherever it landed on the screen.

STOP condition: The participants were told that in some of the trials the dot would jump to another location on the screen and that their job was to pull their hand back immediately when they saw the dot jump and to rest their finger on the response button (waiting until after the second beep before depressing the response button to initiate the next trial).

NOGO condition: The participants were told that in some of the trials the dot would jump to another location on the screen and that their job was to ignore the new location and to touch the screen in the original location, where the dot had been.

Data processing and analysis

Kinematic data were coded within a spatial reference frame having the start button as its origin, in which a straight line path from start button to screen centre defined increasing depth displacement (Y-axis), and a straight line between the left and right target positions defined increasing lateral displacement (X-axis). Raw kinematic data were filtered by a dual pass through a Butterworth filter with a cut-off of 20 Hz. Button release triggered movement recording and defined movement onset. Movement offset was defined as final frame before which forward (Y) velocity fell to zero. In the STOP task, the end of the movement was defined in the same way, and the movement was classified as a successful STOP response if Y-velocity reversed rapidly thereafter, falling below -50 mms^{-1} within at least 50 ms.

The analysis of online corrections in individual jump trials was based upon deviations of the spatial trajectory from the average trajectory for static trials in the same block (see Figure 1). First, the trajectories for all static trials were normalised to 1 mm increments along the depth axis. Second, for each participant, for each trial block, the average lateral coordinate of static trials and its standard deviation were calculated at each depth increment, and cut-offs

were set at 2.81 standard deviations either side of the average. Third, for each jump trial, in each time frame, the movement was classed as corrected if it fell beyond the cut-offs *in the direction of the jump*, being otherwise classed as uncorrected (each comparison thus approximates a one-tailed comparison at alpha ~0.0025). Each jump trial was overall classed as 'corrected' only if it was classed as corrected in the terminal frame of the movement. For these trials, correction time (CT) was estimated as the time at which the last transition from uncorrected to corrected status occurred.

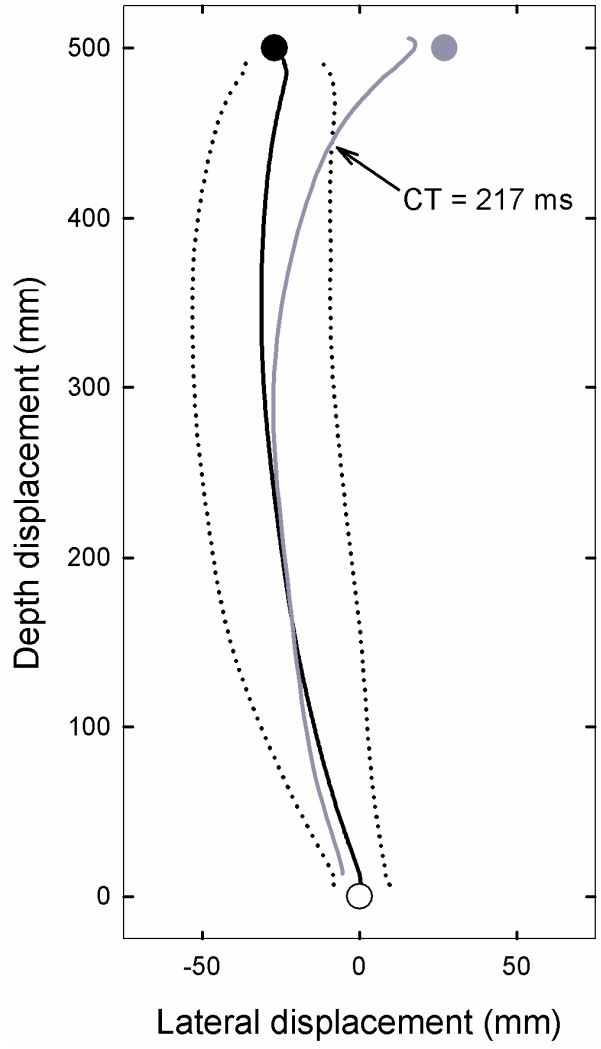


Figure 1. Analysis of online correction in a single jump trial. The solid black trajectory is the average XY path of all of this participant's reaches to static targets on the left of the midline (black circle) in a given reaching condition (e.g. single task, GO instruction). The dotted lines mark a 'bandwidth' of 2.81 SD either side of the average at each depth increment. The grey trajectory is the spatial path of a reach to a target on the left (black circle) that jumps to the right (grey circle) at reach onset. At each time frame, the reach is classed as 'corrected' if it falls outside the bandwidth of static trials, *in the direction of the jump*. In this example, the reach is in a corrected position in its terminal frame, so is classed as a corrected reach. The correction time (CT) is estimated from the time of the last transition from uncorrected to corrected status (217 ms).

Experiment 1: Results

One participant from the NOGO condition was excluded from the analysis. It was not clear whether the participant was unable to follow the task instructions, or did not understand the task requirements, as they produced high rates of corrections towards the new target location in the perturbed trials. As a result, the data from this participant was excluded due to the pattern of responses being different from the other participants in the NOGO condition.

Unperturbed Trials

Movement characteristics on unperturbed trials were used to characterise baseline reaching behaviour. The descriptive data from these trials is summarised in Table 1.

Condition	T1 position	RT	MT	PV	TPV	AE
GO	Left	323.9 (128.3)	429.6 (34.1)	2046.0 (160.7)	126.5 (17.4)	0.0 (0.1)
	Right	320.3 (130.4)	425.3 (35.8)	2123.3 (192.2)	121.5 (16.5)	-0.0 (0.3)
NOGO	Left	342.8 (75.6)	463.7 (107.3)	2049.1 (449.1)	155.3 (67.1)	0.0 (0.1)
	Right	326.6 (73.0)	468.7 (122.7)	2089.5 (474.2)	156.5 (69.7)	0.2 (0.5)
STOP	Left	515.1 (301.9)	459.0 (49.2)	2042.7 (247.5)	129.3 (35.1)	0.0 (0.2)
	Right	512.4 (305.2)	453.1 (50.9)	2123.9 (265.8)	127.1 (32.8)	-0.0 (0.1)

Table 1: Means for the unperturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets).

A mixed-model analysis of variance (ANOVA) was performed separately on reaction time (RT), movement time (MT), peak velocity (PV), time to peak

velocity (TPV) and angular error (AE) with condition (GO, STOP, NOGO) as a between subjects factor and target side (left, right) as the within subjects factor.

There was no main effect of condition for any of the dependent variables [$p \geq 0.11$] which suggests that the participants were behaving in an equivalent manner in all three conditions. There also was no effect of target side in the unperturbed trials for any of the variables, except for peak velocity [$F(1,21) = 21.57$; $p < 0.001$], with higher peak velocities reached to targets on the right. This is expected as the participants responded with the right hand and movements to ipsilateral targets tend to be faster than movements towards contralateral targets (Fisk & Goodale, 1985). A shorter movement time for right-sided targets would also be expected on these grounds, but is not apparent in this experiment. This is most likely due to the small distance (27mm either side of the midline) between the left and right target locations.

Perturbed Trails

The perturbed trials are divided into two categories, (i) those that are classed as corrected and show a deviation towards the new target location, and (ii) those that are uncorrected and do not deviate towards the new target location (see Experiment 1. Methods: Data collection and analysis for more detail). The following perturbed trials analysis uses the corrected perturbed trials only.

Table 2 shows the percentage of perturbed trials that were in a corrected position in the final frame of the movement. As can be seen, there is a low incidence of corrected trials in the NOGO condition. The highest number of corrected trials for targets jumping from left-to-right for any participant was six, with one participant not correcting towards the target perturbation on any trial. For targets jumping right-to-left, the highest number of corrected trials for an individual participant was five, with three participants only correcting on one trial each. This low number of corrected trials in the NOGO condition precludes

the statistical analysis of the kinematic characteristics of corrected movements in this condition, as the estimated means for individual participants would be unreliable. It is also not sensible to directly compare the kinematics of corrected trials in the GO and the STOP conditions, as the GO condition requires the participant to finish with their finger touching the screen and the STOP condition requires the participant to stop their movement when they see the target jump. In order for the movements on perturbed trials in the STOP and GO conditions to be comparable, the movements in the STOP condition would have to have been not successfully stopped. As can be seen from the fourth row of Table 1, there is a low number of corrected but not successfully stopped trials, with three participants always managing to stop their hand in response to a left-to-right perturbation. For right-to-left perturbations, two participants always managed to stop their hand and three were unable to stop on only one occasion each. Due to the low number of unstopped corrected trials in the STOP condition, a between conditions analysis would not be possible, therefore the following analysis of corrected trials is conducted for the GO and STOP conditions separately.

Condition	T1 position	RT	MT	PV	TPV	AE	Percent corrected	Corrected not Stopped
GO	Left	328.1 (126.4)	420.9 (37.1)	2061.8 (197.8)	137.8 (26.6)	-0.0 (0.2)	95.6%	
	Right	318.8 (137.6)	465.9 (49.7)	2057.2 (215.8)	120.6 (12.4)	0.4 (0.6)	83.8%	
NOGO	Left	319.1 (111.1)	514.6 (114.3)	1839.8 (324.1)	180.7 (87.6)	-0. (0.5)	27%	
	Right	295.7 (99.8)	520 (169.7)	2031.4 (542.5)	183.7 (116.5)	0.6 (1.1)	17.6%	
STOP	Left	503.1 (291.9)	399.0 (36.8)	2047.6 (249.9)	130.6 (32.0)	-2. (1.5)	67.1%	11.1%
	Right	464.8 (256.5)	394.3 (43.9)	2094.6 (232.4)	130.6 (31.8)	2.8 (1.5)	69.1%	11.7%

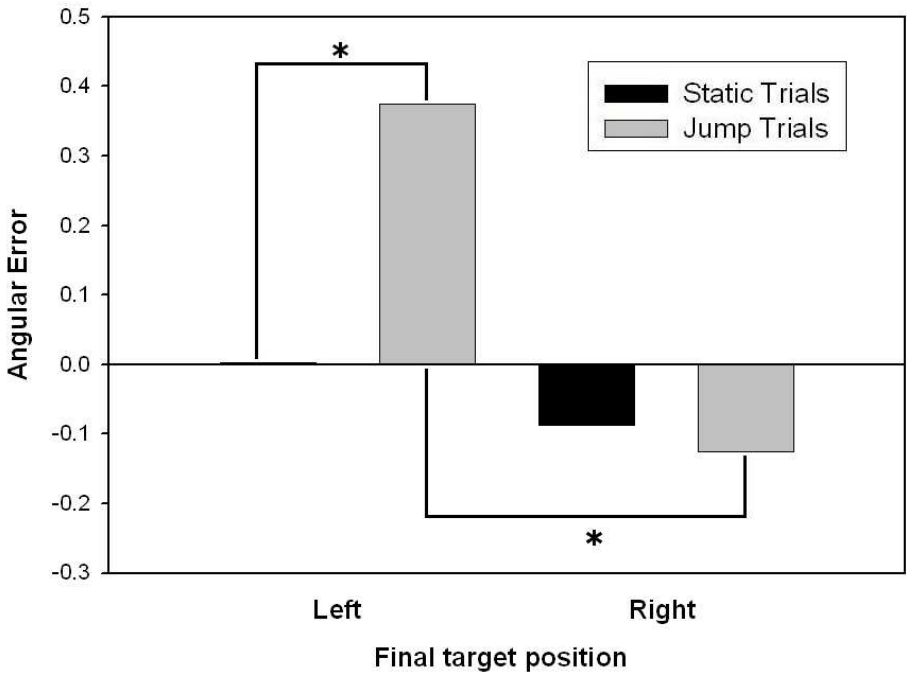
Table 2: Means for the perturbed corrected trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets). The 'percent corrected' column, is the percentage of perturbed trials corrected towards the new target location, and the 'corrected not stopped' column provides the percentage of perturbed trials in the STOP condition during which the participant modified their trajectory towards the new target location but was unable to stop their movement before touching the screen.

GO Condition

A 2 (target 2 location: left, right) x 2 (perturbation: unperturbed, perturbed corrected) repeated-measures ANOVA was performed separately on MT, PV, TPV and AE.

For MT there was a main effect of target 2 location [$F(1,7) = 9.86$; $p<0.05$] and a main effect of perturbation [$F(1,7) = 3.193$; $p<0.05$] in the context of a highly significant interaction [$F(1,7) = 17.62$; $p<0.005$], which reflected longer movement times for movements towards targets that jumped from right to left. Target 2 location had no effect on the peak velocity reached or the time taken to reach peak velocity [$p\geq0.080$]. There was no significant effect of perturbation on any of the other variables [PV, TPV, AE: $p\geq0.405$]. As the perturbation was triggered by movement onset, it would be expected that the planning of the movement on each trial would essentially be the same, as indicated by these results. Any adjustments or corrections made to the planned trajectory occur after peak velocity, during the deceleration phase of the movement.

Figure 2: The mean angular error of perturbed and unperturbed targets in the GO condition.



In the analysis of AE, there was a main effect of side [$F(1,7) = 5.59$; $p \leq 0.05$], again, in the context of a significant interaction [$F(1,7) = 15.43$; $p < 0.05$]. As can be seen in Figure 2, movements towards a stationary target presented on the left resulted in no AE. For target jumps in either direction, the spatial extent of correction was incomplete, in that the final hand position deviated towards the initial target location. However, this was much more pronounced for a target jump to the left, than for a target jump to the right. The MT analysis above revealed that participants were slower moving towards a leftwards jump, and as Figure 2 demonstrates, even with the longer MT, corrections to targets jumping from right-to-left were still hypometric and incomplete, in comparison with the left static trials, although interestingly, the endpoints of corrections towards a rightward perturbed target were equivalent to the right static trials. Post-hoc analysis reveals that there is a significant difference between perturbed and unperturbed trials, when T2 is on the left [$p < 0.05$] and a highly significant difference between the AE for corrected perturbed trials to the right and left [$p < 0.01$].

An analysis of correction time (CT) by direction of jump was performed using perturbed corrected trials. The CT analysis revealed a main effect of direction of target jump [$F(1,7) = 20.17$; $p < 0.005$], with the hand taking longer to arrive in a spatially corrected position for targets jumping from right-to-left. The CT analysis however, cannot reveal whether the corrections for targets jumping from right-to-left are initiated later, or alternatively take longer to show up in the spatial path of the movement, in comparison to corrections for targets jumping from left-to-right (see the Horizontal acceleration section for further discussion).

STOP Condition

A repeated-measures ANOVA of CT by direction of target jump was performed using perturbed corrected trials, as well as Stop time (movement time up to the

point of a zero crossing in the velocity profile indicating the transition form forwards to backwards movement, as the hand is pulled back) and Stop rate (the proportion of successful STOP responses).

CT narrowly failed to reach significance for a main effect of direction of jump [$F(1,7) = 4.35$; $p=0.076$]. Stop time is the movement time for the successfully stopped perturbed trials, but this was not affected by the direction of the jump, neither was the proportion of successfully stopped responses.

	Left → Right	Right → Left
Correction time	295.4 (60.5)	304.9 (63.8)
Stop time	401.0 (58.9)	405.4 (69.9)
Stop rate	83.5%	83.0%

Table 3: Mean correction time and mean stop time in corrected and stopped perturbed trials (ms) and percentage stop rate in corrected perturbed trials. (Standard deviations given in brackets).

In addition to the CT analysis in the GO condition, the fact that there was no main effect of the direction of the jump for the Stop time suggests that the target jump is not detected any earlier on the right side in comparison to the targets on the left. Although not detected earlier, there is still a difference in the GO condition which suggests corrections towards the right are executed with more efficiency.

Individual Corrections

Figure 3 is compiled using the individual rates of corrections for each participant, computed as described in Experiment 1. Methods: Data collection and analysis.

Figure 3: The mean rates of individual bilateral current corrections for the GO, NOGO and STOP conditions. (a) denotes the time at which the GO and the NOGO conditions are significantly different from each other, (b) is the time at which the GO and STOP conditions are significantly different from each other, and (c) is the time at which all three conditions are significantly different from each other

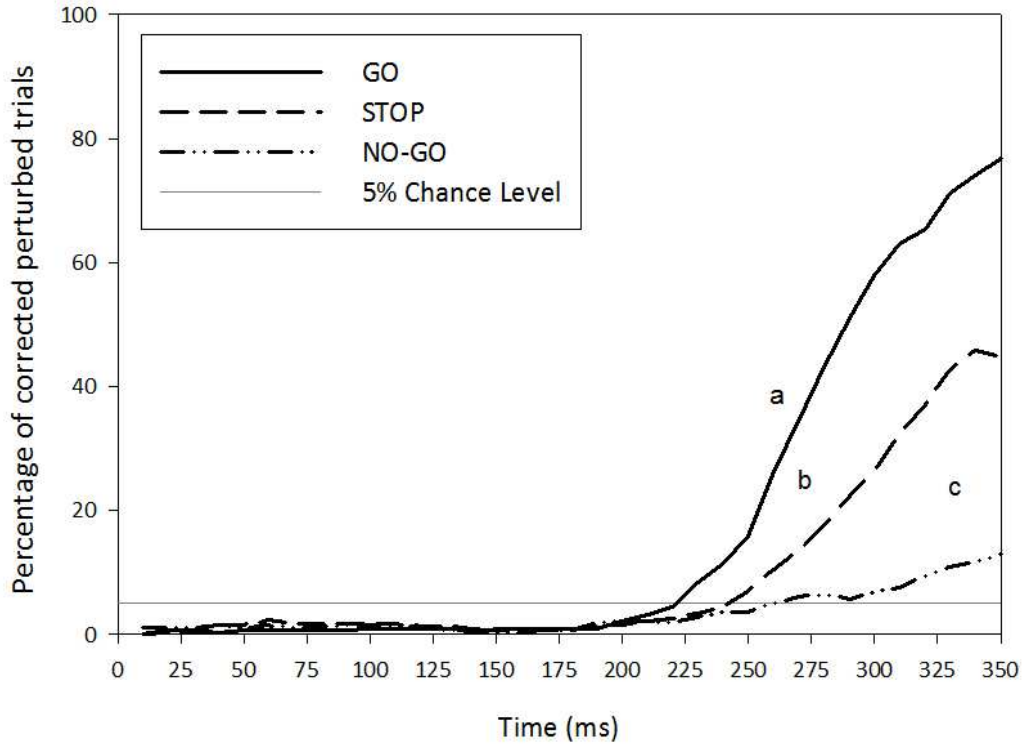


Figure 3 shows that there are low rates of corrections in the NOGO condition and high rates in the GO condition. This would be expected, as the task instructions require the participants to follow the direction of the target perturbation in the GO condition and to ignore the target perturbation and continue to the original location of the target in the NOGO condition. In the STOP condition, without explicit instructions to either follow or ignore the target jumping, the participants still made corrections towards the direction of the jump in nearly 45% of trials. The rates of corrections exceed the 5% chance level just after 220ms in the GO condition, just before 245ms in the STOP condition and just past 260ms in the NOGO condition. Participants in the GO condition, as well as making more corrections, appear to begin to correct slightly earlier in their movements than those in the NOGO and STOP conditions.

This observation is consistent with the results of the CT analysis; however the earlier appearance of corrections in the GO condition could be due to shorter latency or increased vigour of reacceleration, driving the hand to a corrected position at an earlier time. The analysis of horizontal acceleration profiles suggests that the second explanation may be more likely (see below).

A mixed-model ANOVA was performed on the rate of individual corrections for each 10ms bin up to 350ms (35 levels), with condition (GO, STOP, NOGO) as a between subjects factor and direction of jump (left-to-right, right-to-left) as a within subjects factor.

In order for any effect to be considered, it had to remain significant for 50ms (10 consecutive temporal bins). At 260ms, the effect of condition becomes reliable [$p \leq 0.016$], with the GO and NOGO conditions significantly different from each other (see Figure 3) and from 270-310ms the GO and STOP conditions are also significantly different from each other [$p \leq 0.045$], with all conditions significantly different from each other by 330ms [$p \leq 0.049$]. Between 260ms and 340ms there is a main effect of the direction of the jump [$p \leq 0.034$], with more corrections for targets jumping from left to right, and a reliable condition x direction of jump interaction between 260 and 300ms [$p \leq 0.049$], with more corrections in GO condition for targets jumping left to right.

Horizontal Acceleration Profiles

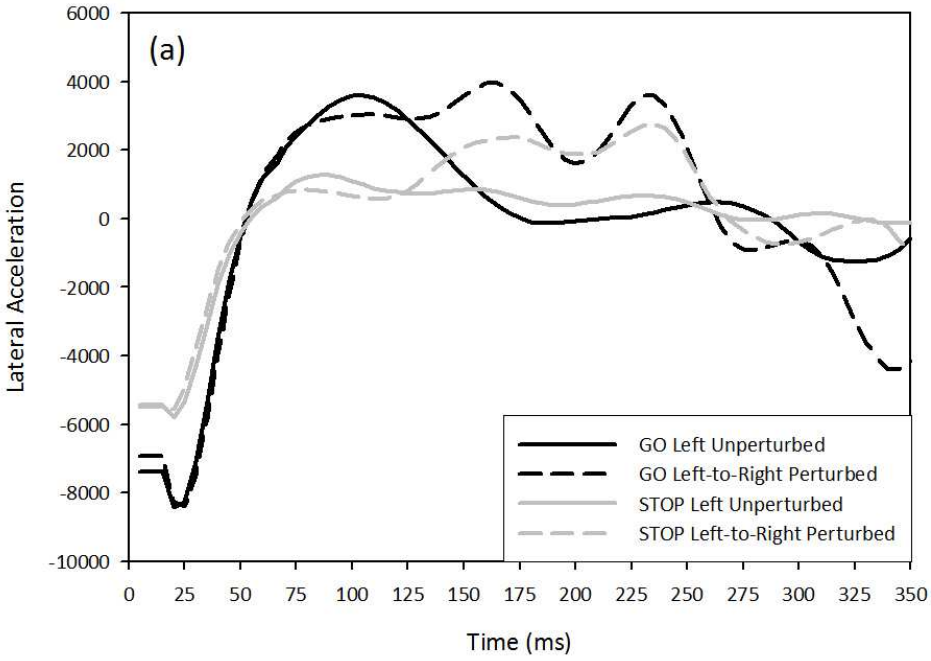
The purpose of the horizontal acceleration analysis is to identify the time at which the corrections occur, by detecting the time at which the hand accelerates in a sideways direction towards the new target. This particular analysis allows the identification of the onset of corrections across the participants, at a population level. The horizontal acceleration analysis is different to the CT analysis, as the CT is considered as the time at which the hand's trajectory

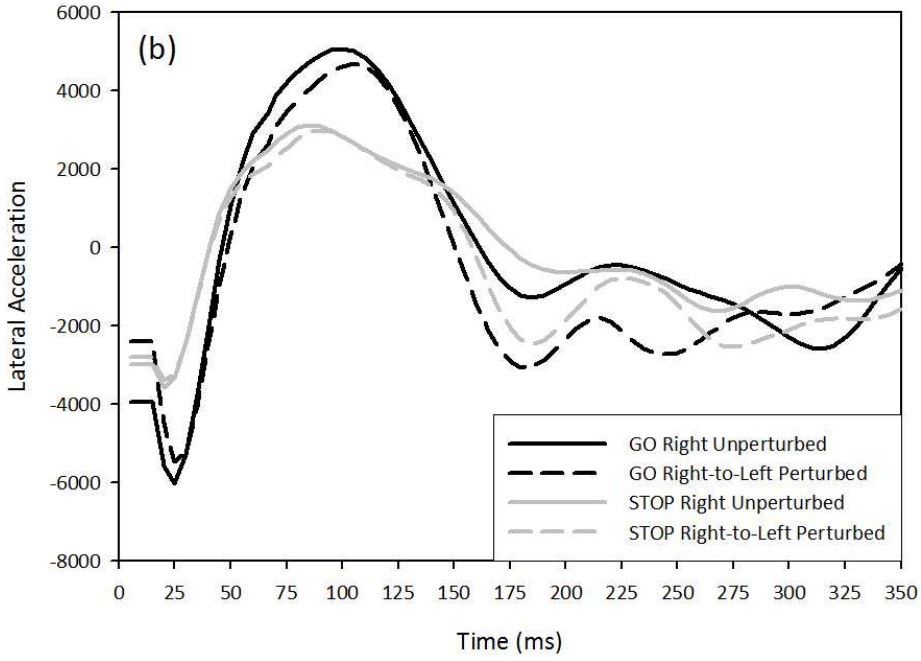
crosses the bandwidth created by the unperturbed trials. These corrections will have been initiated earlier than the CT analysis can reveal, as it takes time to show up on the spatial analysis, and by analysing the timing of the additional horizontal acceleration, it is possible to identify the time at which the correction was initiated towards the new target location. As in the perturbed analysis, the number of corrected perturbed trials was too low in the NOGO condition to be included in the analysis (see Table 2). Therefore, the analysis of the horizontal acceleration profile contains trials from the GO and STOP conditions only.

A repeated-measures ANOVA was performed on horizontal acceleration with condition (GO, STOP) as a between subjects factor and perturbation (unperturbed, perturbed corrected) as the within subjects factor. As with the individual corrections analysis, in order for any effect to be considered it had to remain significant for 50ms.

For targets that jumped from left to right, corrections occurred at 135ms [$p \leq 0.018$] (see Figure 4a). This was the same for both the GO and the STOP conditions, as there was no significant interaction with condition for any time bin. The correction occurred with the same latency for both the GO and the STOP conditions. The pattern is similar for targets that jumped from right to left, with corrections occurring at 140ms [$p \leq 0.048$], as can be seen in Figure 4b. Again, this was the same for both the GO and the STOP conditions, as there was no significant interaction, demonstrating the correction latency was similar for the GO and the STOP conditions.

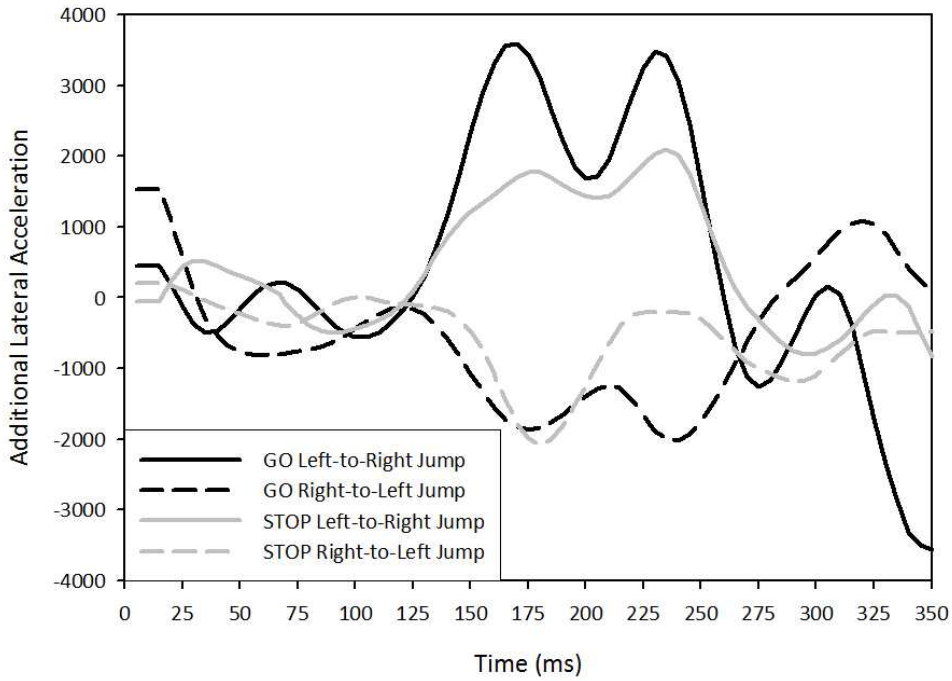
Figure 4: The mean horizontal acceleration profiles for movements towards targets initially presented on (a) the left and (b) on the right under the GO and STOP condition instructions. The unperturbed trials are plotted in solid lines and the perturbed corrected trials are plotted in the dashed lines, with trials in the GO condition plotted in black and trials in the STOP condition presented in grey.





When directly comparing the corrections to left and right perturbed trials (as a difference from the baseline) in a 2 (condition: GO, STOP) x 2 (direction of jump: left, right) repeated-measures ANOVA, there was no significant effect of condition, no significant effect of side and no interaction. This result suggests that there is no difference between the GO and the STOP conditions in the timing of the acceleration in either the left or right horizontal direction, as can be seen in Figures 4a and 4b. Even though Figure 5 demonstrates the greater amplitude of the corrections, and more vigorous changes in direction in the GO condition in comparison to the STOP condition, especially for target perturbations towards the right, the horizontal acceleration analysis shows that the latency of the corrections is occurring at a similar time in both conditions.

Figure 5: Additional horizontal acceleration profile for corrected trials relative to unperturbed trials in the GO and STOP conditions.



Summary

The above analyses provide a profile of the automatic pilot operating under different conditions. The individual corrections analysis revealed that there were high rates of correction in the GO condition, moderate rates of correction in the STOP condition and low rates of correction in the NOGO condition. Since no instructions regarding online correction were given to participants in the STOP condition, we may assume that the moderate level of online correction in this condition represents the default response of the automatic pilot. The results of the GO and NOGO condition therefore imply that this default level of responsiveness can be voluntarily enhanced by the instruction to correct and, even more importantly, overridden by conscious instruction. The automatic pilot therefore fails to satisfy the intentionality criterion, and is only weakly, not strongly automatic.

There appears to be a general difference between the ability to correct to targets which jump to the left and the right, with the right hand. Movement times in the GO condition were longer to targets which jumped from the right to the left, and also the endpoint error was larger for leftwards perturbations, indicating that even though the system took more time to arrive at the left target location, it was less accurate. Although the movement times towards leftwards jumping targets were longer and the CT was later, the horizontal acceleration analysis demonstrates that the correction within the movement is not initiated any later, with no difference between the correction latency for left and right target jumps. This indicates that ipsilateral corrections may be implemented with more vigour, presumably due to hemispheric and/or biomechanical compatibility for movements towards targets on the same side as the responding hand (e.g. Fisk & Goodale, 1985).

Experiment 1: Discussion

Experiment 1 set out to investigate the automaticity of movement corrections in manual aiming movements, using kinematic analysis. This study employed the GO and STOP responses already established in the literature, as well as introducing a new NOGO instruction, which required participants to point to the original location of the target even if the target was perturbed. The main finding of this study is that corrections made towards a target perturbation may indeed be 'weakly' automatic, in the sense that they occur when uninstructed (STOP condition), but are not found to be 'strongly' automatic, as they can be suppressed using voluntary control (NOGO condition), and therefore do not meet the intentionality criterion for automaticity. This is evident in the low number of corrected perturbed trials in the NOGO condition, as can be seen in Table 2. The low rates of corrections in the NOGO condition demonstrate that participants are able to follow task instructions and resist the target perturbation and continue to the original target location. However, when given no instruction other than to abort their movement upon target perturbation, participants do move towards the new target location before pulling their hand back. These rates of correction, however, are not as high as in the GO condition, in which the instruction to follow the target resulted in high rates of correction, demonstrating that the responsiveness of the autopilot can be voluntarily enhanced when required.

In 45% of perturbed trials in the STOP condition, the participants were in a corrected position before they were able to pull their hand back, a finding which closely matches Cressman et al's (2006) rate of 42%. Also similar to the Cressman et al. (2006) study is the use of kinematic analysis, which allowed the analysis of successfully stopped, and therefore uncompleted movements and is sensitive to spatial deviations in the trajectory (Cressman et al., 2006). In the Pisella et al. (2000) study, automatic corrections were established using

movement endpoints, and although their methodology of using different movement times provided replicable results, it could potentially lead to an underestimation of the numbers of corrections to perturbed targets, as they were drawn from averages across all of the time bins investigated. The Cressman et al. (2006) study and the current experiment report rates of correction that are higher than those reported by Pisella et al. (2000) and are able to demonstrate that the hand, especially in the STOP conditions, can be in a corrected position before the movement is aborted: Data which is unavailable in the solitary analysis of endpoints.

The demonstration that the hand is in a corrected position before the movement is stopped during the STOP condition supports the argument for the automatic pilot being in-part automatic. These corrections occur even though they are uninstructed, but not to the same extent as they occur in the instructed GO condition. This is evident in the horizontal acceleration analysis and Figures 4a, 4b, and 5. In all three figures, the horizontal acceleration of the hand in the GO condition appears greater than in the STOP condition, and although this difference is not significant in respect to the time that the corrections occur, the strength of the corrections appears amplified by the conscious decision or instruction to make them. It thus appears that the voluntary enhancement of the automatic pilot operates via increased vigour (and frequency) of corrections, rather than a reduced response latency.

If the rates of corrections in the GO condition are boosted by the intention to correct, then performance in the NOGO condition could also be driven by the conscious intention *not* to correct. If both the GO and the NOGO conditions require conscious processes to produce the performance seen in the current experiment, it would be interesting to place the system under dual task conditions and monitor the rates of corrections produced when limited cognitive resources are available. Further to this point, if the GO and the NOGO conditions require additional processes, does that make the STOP condition the

default system behaviour? The rates of corrections in the STOP condition could be a demonstration of the baseline level produced automatically by the automatic pilot under no specific task requirements. The influence of cognitive resources on the online correction of manual aiming movements is explored further in Experiments 3 and 4.

A second question of interest, which arises from the data, would be to closely examine the relationship between the direction of the target perturbation and hand used to perform the aiming movement. In Experiment 1, participants were all right handed and all performed the task using their right hand. MT, AE and CT were all significantly greater for target perturbations from right-to-left in comparison with target perturbations from left-to-right, although the horizontal acceleration analysis suggests that there is no difference in the latency of the corrections produced on either side. The difference between movements to the left and the right occur after peak velocity has been reached, in the deceleration phase of the movement. Day & Lyon (2000) also found more deviation towards right targets in participants using their right hands. Rightwards moving targets produce a higher rate of corrections with the right hand, and it would be interesting to confirm whether the reverse is true for aiming movements made by the left hand towards left moving targets, and whether this is a simply due to biomechanical and/or hemispheric compatibility effects, privileging ipsilateral over contralateral movements (e.g. Fisk & Goodale, 1985). This is explored in Experiment 9.

The current study has replicated Pisella et al.'s (2000) and Cressman et al.'s (2006) STOP findings, with moderate rates of uninstructed corrections, however, the new contribution to the literature is the finding that these uninstructed corrections can be almost abolished if the participant is explicitly instructed to do so. The NOGO task differs from the STOP task and the online anti-pointing task (Day & Lyon, 2000; Johnson et al., 2002) in that it is a direct, conscious response that requires the motor program to remain the same. The

ability to produce this response and not to correct towards the new target location demonstrates that although the automatic pilot may be automatic in the sense that it operates without instruction, the automatic pilot is not insensitive to conscious instruction and can be overridden when required. Successful NOGO performance does not lead to intentional conflict, as observed by Johnson et al. (2002) in their anti-pointing task, as there is no conflict. The task in the NOGO condition is to continue with the original motor program, rather then identify the new target location and program a new movement in the opposite direction, as is the task in the online anti-pointing task.

In the STOP and anti-point tasks, the target jump is a signal that is tied into the required task response, whereas in the NOGO task, the target jump signal is irrelevant to successful task completion (Cameron, Cressman, Franks & Chua, 2009). Since the set of experiments reported in this chapter were carried out, two papers have been published which has also employed close variants of the NOGO task instruction. Cameron et al. (2009) investigated the influence of an instruction to IGNORE the target perturbation on the rates of online correction. They reasoned that if in the IGNORE task, the target perturbation signal was irrelevant to task performance, then the power of the 'jump' signal could be reduced by asking participants to ignore it. As in the current experiment, Cameron et al. (2009) reported low rates of correction in the IGNORE condition in comparison with the GO and the STOP conditions. Striemer, Yukovsky, and Goodale (2010) subsequently used a similar task, instructing participants not to correct the movement if the target jumped, but to continue reaching to the initial target position. This NOGO instruction led to a substantial reduction of corrections relative to a GO task (32 vs. 64%), confirming the general finding. However, whereas Experiment 1, like Cameron et al. (2009), found a near-total elimination of corrections (7%), Striemer et al. found an appreciable residual rate (32%). The likely reason for the differing rates of unsuppressed corrections is that these studies differed in the predictability of the jumped target location. Experiment 1, like Cameron et al. (2009), used two target locations only, so a

target on the left could only jump to the right and vice-versa. In Striemer et al.'s (2010) design, any target could jump either left or right, and much higher rates of unsuppressed corrections were observed. If the NOGO task is solved by inhibiting orienting responses to the jumped target, this may be better achieved when its location is predictable, as only one location need be inhibited.

The GO and STOP instructions require participants to monitor the target for a change in location, where as the NOGO instruction does not. It is not necessary to attend to the target once the movement has been initiated, as the NOGO task instructions require the participant to point to the original location of the target. Whether or not the target is perturbed is irrelevant, as the movement would be aimed at the same location. One possible criticism of the current study is the opportunity for participants to complete the NOGO task by ignoring visual information from the very start of the movement, as the T1 target location is presented when the button is depressed. Experiment 2 provides a control for such behaviour.

Experiment 2: Introduction

The NOGO instruction, introduced in Experiment 1, requires a control experiment to ensure that participants in the NOGO condition are able to complete the pointing task in the same way as participants in the GO and STOP conditions. The low rates of corrections produced under the NOGO task instruction observed in Experiment 1 have since been replicated by Cameron et al. (2009), with similarly low rates of corrections produced when the participant is instructed not to make corrections. In the Cameron et al. (2009) study, the authors suggest that the low rate of corrections in the IGNORE condition result from the automatic response to the target jump (i.e. the desire to follow the target) being inhibited before each trial. One of the suggestions

they put forward as a method of inhibition is the suppression of specific visual input and the sole focus of attention being placed on the initial target location.
As described, it could be possible for participants in the NOGO condition to mentally disengage from the task once the location of the T1 stimulus had been identified. In this situation, the participant could push down the button, see the target and then launch a movement towards that (remembered) location and ignore any visual information once the movement had been initiated: There would be no need to ignore the target jumping or to override any desire to follow the jumping target with the hand. This strategy, however unlikely, would allow the participant to push down the button, see the target on the screen and then move towards the target having mentally disengaged from the task, as no other information about the target would be necessary to fulfil the requirements of the NOGO task. One way to control for this withdrawal of visual attention is to use an embedded visual discrimination task, which would require participants to pay attention to the target and still resist the pull of the perturbed target.

Experiment 2 provides this control by way of a two-stage, between-subjects pointing task. In the first stage, a letter detection task was also presented in the T2 stimulus on all unperturbed trials. The requirement of the detection and identification of the letter would not allow the participant to withdraw visual attention from the target stimulus, but would demonstrate that participants are able to attend to the target within a narrow focus of attention. If participants are able to correctly report the letter in the target and still show low rates of correction, this would demonstrate the ability to narrow the focus of attention and to switch off the automatic pilot to stimuli and events occurring outside the focus of attention, as required. This task however, could still be performed by monitoring only a small section of space, and so there would be no need to detect and jump and then ignore it. The task could be performed by only monitoring the target location and if the target disappears, it doesn't matter where to, as the task is to point to the original location.

In order to control for the alternative strategy of narrowing visual attention to only the T1 stimulus location, the second stage of the control task was to present the letter detection task in the T2 targets on all trials, both unperturbed and perturbed. In order to complete the task, the participant would need to attend to the T2 stimulus in the perturbed location, but still continue to point to the original location of the T1 stimulus. If this task is performed successfully, then it would demonstrate that participants are able to acknowledge the target perturbation and still successfully override the mechanism to correct towards the new target location, supporting the explanation that the motor responses towards the jumped target are inhibited, rather than the target stimulus filtered by visual attention.

Experiment 2: Methods

Participants

Sixteen naïve adult volunteers (13 females and 3 males, mean age: 23.13 years, SD: 5.16) took part in the study. The participants were recruited using the same procedure as detailed in Experiment 1. All of the participants were right-handed and reported no visual or motor deficits, and were allocated, in rotating order, to the two experimental groups.

Design

The design of the study was the same as in Experiment 1, except it consisted of two between-subjects conditions, the 'Unperturbed Trials' condition, and the 'All Trials' condition. In the Unperturbed Trials condition, a letter detection task composed of an E or inverse-E was presented in the centre of the target in the T2 position in only the unperturbed trials. In the All Trials condition, the letter

detection task was presented in the centre of the target in the T2 position in all of the trials, both unperturbed and perturbed. The participant was required to identify the letter within the target and to verbally report the identity of the letter to the experimenter, to be input by keyboard.

Apparatus

The apparatus was the same as used in Experiment 1. In addition, the T2 stimulus contained a 3mm x 4mm black E or inverse-E presented in the centre of the dot, which was presented for 350ms.

Procedure

The procedure was the same as the NOGO task instructions in Experiment 1. Additionally, at the end of each trial, the participant is required to report whether an E or an inverse-E was presented in the centre of the second target and the response is input by the experimenter.

Experiment 2: Results

Letter detection task

Performance on the letter detection task was recorded for each trial and the percentage of correct performance is displayed in Table 4 across all participants in each condition. As can be seen, participants were able to correctly discriminate the orientation of the letter in the T2 stimulus on a high percentage of the trials.

Condition	Unperturbed Trials		Uncorrected Perturbed Trials		Corrected Perturbed Trials	
	T1 Left	T1 Right	T2 Right	T2 Left	T2 Right	T2 Left
All Trials	96.1	94.4	94.1	92.4	87.0	95.1
Unperturbed Trials	92.8	93.8				

Table 4: The percentage of correct performance on the letter detection task for the unperturbed trials, the uncorrected perturbed trials and the corrected perturbed trials in both the All Trials and Unperturbed Trials conditions

Reaching Task: Unperturbed Trials

A mixed-model ANOVA was performed separately on RT, MT, PV, TPV and AE with condition (All Trials, Unperturbed Trials) as a between subjects factor and target side (left, right) as the within subjects factor.

There was no main effect of condition for any of the dependent variables [$p \geq 0.082$] which suggests that the participants were behaving in an equivalent manner in both conditions. There also was no effect of target side in the unperturbed trials for any of the variables, except for peak velocity [$F(1,14)=37.894$; $p<0.001$], with higher peak velocities reached to targets on the right. This finding precisely replicates the pattern of results for the unperturbed trials in Experiment 1.

Condition	T1 position	RT	MT	PV	TPV	AE
All Trials	Left	648.9 (317.6)	434.3 (68.7)	2216.1 (306.9)	131.9 (34.9)	-0.1 (0.3)
	Right	651.4 (314.2)	434.0 (73.7)	2275.4 (340.6)	129.7 (35.5)	0.3 (0.4)
Unperturbed Trials	Left	512.9 (221.4)	472.1 (51.2)	1849.1 (233.8)	139.3 (27.8)	-13.9 (37.1)
	Right	511.9 (212.1)	467.9 (52.1)	1931.2 (221.7)	135.7 (23.0)	0.9 (2.1)

Table 5: Descriptive statistics for the unperturbed trials in the All Trials and Unperturbed Trials conditions.

Reaching Task: Perturbed Trials

The current experiment employed only the NOGO task instruction across both conditions, and thus there are very few corrected perturbed trials available for analysis, replicating the findings from Experiment 1 despite the additional letter detection task. The following perturbed trial analyses are therefore carried out using the perturbed trials that were not corrected towards the new target location. If participants are able to override the intention to correct towards the new target location then it would be interesting to compare the movements directed towards the same location on the perturbed and unperturbed trials.

Condition	T1 position	RT	MT	PV	TPV	AE	Percent uncorrected
All Trials	Left	672.0 (287.5)	457.4 (101.8)	2174.2 (303.3)	136.3 (37.1)	-6.1 (0.3)	85.5%
	Right	625.3 (284.0)	443.1 (71.7)	2260.1 (305.6)	134.1 (30.7)	6.5 (0 .6)	74.2%
Unperturbed Trials	Left	543.0 (231.0)	532.6 (132.0)	1836.4 (343.9)	165.0 (61.3)	-5.8 (0.7)	67.7%
	Right	541.0 (249.2)	510.6 (94.0)	1857.6 (285.0)	131.6 (19.5)	-6.6 (35.2)	53.8%

Table 6: Descriptive statistics for the uncorrected perturbed trials in the All Trials and Unperturbed Trials conditions.

A mixed-model ANOVA was performed separately on MT, PV, TPV and AE, with target 2 location (left, right) and perturbation (unperturbed, perturbed uncorrected) as within subjects factors and condition (All Trials, Unperturbed Trials) as a between subjects factor.

There was no effect of condition on any of the dependant variables, which again suggests that the participants were behaving in an equivalent manner in both conditions. Again, as with the unperturbed trials, there was a significant effect of target 2 location on the peak velocity reached during the perturbed trials, with higher peak velocities in trials when the target jumped rightwards

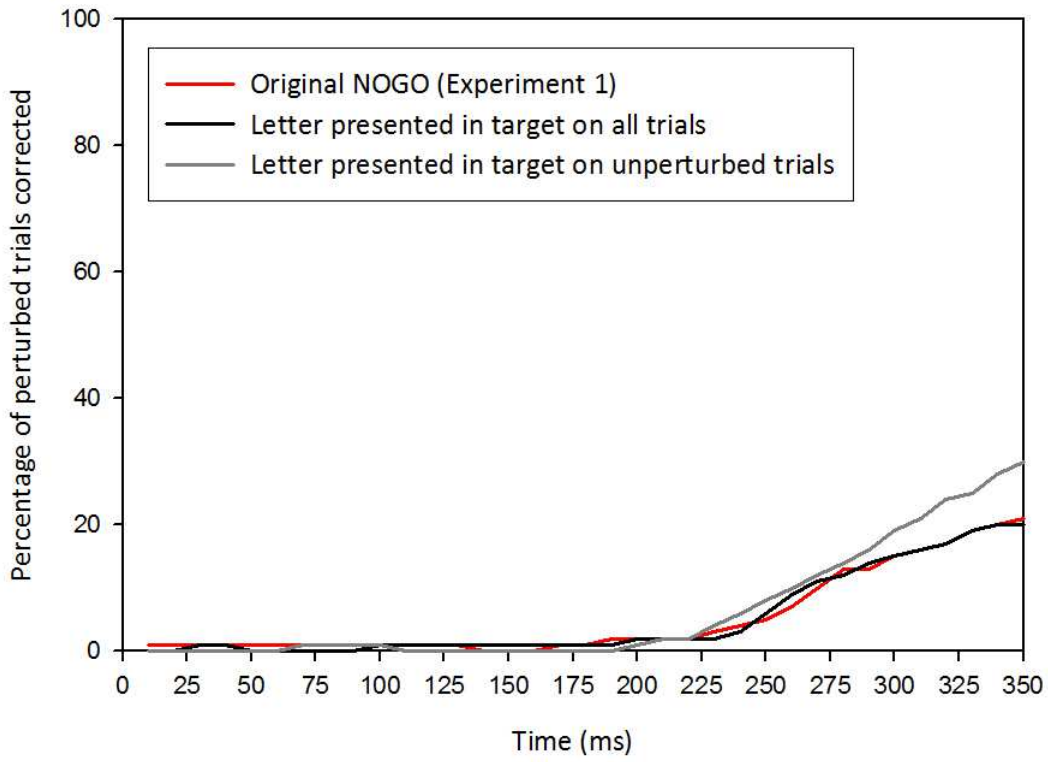
[F(1,11)=15.700; p<0.005]. There was also a trend, which narrowly failed to reach significance, for a main effect of perturbation on the movement times [F(1,11)= 4.504; p=0.057], with faster movement times towards the target in the unperturbed trials. There were no main effects or interactions for the time to reach peak velocity.

In the analysis of AE, there was both a main effect of target 2 location [F(1,13)=10.82; p<0.01], with more error for targets presented on the left or jumping from left-to-right, and a main effect of perturbation [F(1,13)=16.698; p≤0.001], with more error in the perturbed trials than the unperturbed trials. Although the endpoint of the movement was less accurate in the perturbed trials, the finishing location of the finger was still within the bandwidth created by the trajectories of the unperturbed trials.

Individual Corrections

A 2 (target 2 location: left, right) x 2 (condition: All Trials, Unperturbed Trials) mixed-model ANOVA, performed on the individual rates of corrections produced by participants for each 10ms time bin (35 levels), revealed that there is a significant effect of target 2 location from 270ms [p≤0.002], with more corrections towards rightwards target perturbations. There is no effect of condition on the rates of corrections produced, demonstrating that whether participants were required to monitor the target for the letter on all of the trials or just the unperturbed trials, they are still able to perform the task following the NOGO instruction equally as well. This is demonstrated in Figure 6, with the bilateral individual rates of correction plotted. In addition, the bilateral rate of correction of the NOGO condition in Experiment 1 is also plotted in red for comparison, to show the similar low levels of correction produced in both experiments.

Figure 6: The mean rates of bilateral individual current corrections for the All trials and the Unperturbed only conditions. Also plotted for comparison in red is the bilateral individual correction rate from the NOGO condition in Experiment 1.



Summary

The results from Experiment 2 replicate those from Experiment 1, in terms of both the pattern of kinematic results and the rates of individual corrections, and provide evidence that participants are able to follow the NOGO instruction. Although there is individual variability in performance, the participants on the whole were able to follow the NOGO task instruction and not make many corrections towards a perturbed target, even when they are required to monitor the target at the new location. Experiment 2 provides evidence that participants are able to pay attention to the target at the new location and still override the need to correct towards the target.

Experiment 2: Discussion

Experiment 2 was run as a control experiment for the NOGO condition, introduced in Experiment 1. The purpose of the experiment was to check whether participants were using a different strategy to perform the NOGO task, compared to the assumed behaviour of participants in the GO and STOP conditions. In the GO and STOP conditions, the participant is required to monitor the target once the movement has begun, in case the target jumps to a new location during the movement, in order to successfully complete the task, and either adjust their ongoing movement towards the new target location or abort their movement and pull their hand back to that starting position. In the NOGO condition, it could be suggested however, that once the target has been presented and the participant knows where the target is on the screen, it is unnecessary for the participant to monitor the target, as their task is to point to the original location of the target. Whether the target is perturbed or not is almost irrelevant, as the movement that should be initiated would be to the same location.

Experiment 2 provides evidence that participants were able to follow the NOGO task instruction, even when they are required to monitor the target at the new location. The important outcome of the current experiment is that there was no difference between the two conditions, which would therefore suggest no difference in the strategies employed by the participants for successful task completion. The level of corrections produced in the two conditions were at a similar rate to those produced in the original NOGO condition in Experiment 1 (see Figure 6), implying that this conclusion can be generalised to the original NOGO data in Experiment 1. Experiment 2 provides evidence that participants are able to monitor both the original target location and the target at the new location, through correct identification of the letter in the embedded visual discrimination task, without resulting in the hand deviating towards the target

at the new location. Admittedly, the attentional discrimination required in this task was relatively easy, since the letter remained visible during the 350 ms that T2 was onscreen. It is therefore conceivable that participants could have withdrawn their attention from the screen during the early part of the reach (when the jump would occur), but thereafter reallocate their attention to discriminate the letter, and still achieve high discrimination accuracy. Given this possible limitation, the present results should perhaps be regarded as suggestive, rather than definitive.

The NOGO instruction has been demonstrated as an effective tool to investigate the automaticity claims of the autopilot phenomenon, with Cameron et al. (2009) observing similarly low rates of corrections produced when the participant is instructed not to make corrections. The current control experiment expands the findings of the Cameron et al. (2009) study, and argues against the suggestion that the automatic response to the target jump is inhibited via the suppression of visual input, with the sole focus of attention being placed on the initial target location. In the current control experiment, participants are able to attend to the target in the new location and still inhibit the corrective response towards that location.

The control experiment for the NOGO condition also replicates other aspects of Experiment 1, as the difference between the movements and corrections towards rightwards and leftwards presented targets is evident in the current experiment, as is an individual variability in the ability to perform the task successfully. In Experiment 1 one participant from the NOGO condition was excluded from the analysis, for seemingly not complying with the task instructions. Following the examination of the variability in participants' abilities in the current experiment, this individual may not have been able to follow the NOGO task instructions. The higher rate of corrections produced by this particular participant was in direct contrast to those produced by the other

participants in the NOGO condition, and similarly high rates are also evident in two of the participants in the current experiment.

The issue of individual variability has been observed and discussed by other research groups investigating online control of aiming movements. Veerman, Brenner & Smeets (2008) observed noticeable variability between participants in their study. Each participant completed pointing movements in 12 different target attribute conditions, yet the variability between individual performances was greater than the variability between conditions. This variability was stable for each participant, and if a participant was slow to initiate corrections in one condition, then they were slow in all other conditions as well. It appears that some people are just better than others at this type of task, and are quicker to respond, quicker to correct, and are more likely to correct towards a target. Veerman et al. (2008) suggest this is why some people are better at certain sports, due to 'differences between their minimal visuomotor latencies' (p. 227). The variability in performance demonstrated in the current experiment supports this conclusion.

Experiment 3: Introduction

The findings from Experiment 1 suggested that the STOP response may reveal the default setting of the automatic pilot, as there were no specific instructions. Furthermore, the rates of correction differed from the uninstructed rate under instructions to actively make corrections or to suppress them. As already discussed, the moderate rate of corrections produced in the STOP condition occur even though the corrections are uninstructed, a finding replicated in the literature (Pisella et al., 2000; Cressman et al., 2006). As revealed by the horizontal acceleration analysis, the latency at which these 'default' corrections are initiated is no different from the corrections produced under the GO

instruction. Although the timing of the corrections is similar, the corrections made are more vigorous in the GO condition, and this additional strength in the correction may be due to the instruction (and/or desire) to move towards and follow the target.

The GO instruction provides the intention to go and results in an increased rate (and a possibly an increased magnitude) of corrections, and the intention to not follow the target under the NOGO instruction results in the reduced rate of corrections, in comparison with the STOP instruction. The observed changes in performance between conditions in Experiment 1 are due to the intention of the participant, as determined by the task instructions, highlighting that this behaviour fails to meet the intentionality criterion required to identify the behaviour as automatic. Experiment 1 revealed that the presumed automatic behaviour of correcting towards a new target perturbation is indeed sensitive to voluntary control. The second criterion for automaticity is that the process must be insensitive to a concurrent cognitive load. If the GO and NOGO task performance observed in Experiment 1 was due to the intention of the participants, the question remains whether the intention is effortful and requires cognitive resources to be maintained?

One way to attempt to answer this question is to use a cognitively demanding task concurrently with the manual aiming task. Importantly, the secondary task should differentiate from the visuomotor task, as direct competition for the dorsal stream processes that support online correction would need to be avoided. Cameron et al. (2007) demonstrated that correction efficiency is reduced when participants reach in sequence to two visual targets, either of which can jump at movement onset. In the Cameron et al. (2007) study, the reduced responsiveness of the automatic pilot reflects visuomotor processing load in dual-target relative to single-target conditions. By contrast, the focus in the current experiment is to identify the influence of a non-visual, non-motor cognitive task on correction performance. The auditory n-back task was

selected, as it has successfully been used as a secondary task for both visual and motor studies (Mitchell, Macrae & Gilchrist, 2005; Voelcker-Rehage & Alberts, 2007). Boot, Brockmole and Simons (2005) found that when participants were required to listen to a string of numbers and count the number of sequential repetitions whilst performing a visual search task, the rate of attentional capture by abrupt onsets was reduced. Boot et al.'s (2005) visual search task requires a relatively low level attentional ability, which is perhaps similar to the kind of 'capture' observed in the double step task, hence the decision to use the same task in the current experiment.

Hypothesis

If the level of corrections produced in the STOP condition is the default level produced by the automatic pilot and the GO and NOGO rates of correction responses require effort to be maintained, then it would be hypothesised that under dual task conditions, with a demanding cognitive load, the rates of correction in the GO and NOGO condition would converge towards the levels of correction produced in the STOP condition. More specifically, it would be expected that the rates of correction in the GO condition would reduce, and the NOGO correction rates would increase towards the presumed default rate of corrections produced in the STOP condition. Furthermore, if correction rates in the STOP condition do indeed represent the default behaviour of the automatic pilot, then the dual task condition would not be expected to affect correction behaviour in the STOP condition.

Experiment 3: Methods

Participants

Twenty-four naïve adult volunteers (18 females and 6 males, mean age: 21.17 years, SD: 2.24) took part in the study. The participants were recruited using the same procedure as detailed in Experiment 1. All of the participants were right-handed and reported no visual or motor deficits, and were allocated, in rotating order, to one of three groups.

Design

The study consisted of three between-subject conditions, the GO condition, the STOP condition and the NOGO condition. Each condition was made of two experimental blocks of 100 trials, with 5 practice trials before each block. One block was performed under single task conditions and the other under dual task conditions, with order of blocks counterbalanced across participants. As in the previous experiments, there were two possible target presentation locations, on the left and the right, with the target jumping to the left or right an equal number of times on the perturbed trials. Each block had a 30% perturbation rate, and on the further 70% of trials, the target remained stationary when the participant released the button. On all trials, the target was presented on the right in 50%, and on the left in the other 50% of trials. Stimuli were presented in a random order and a break was given to the participant between blocks. At the end of the second block, eight calibration trials were recorded, to provide reference points for the calculation of spatial errors.

Across all conditions and both experimental blocks, there was a concurrent auditory 1-back task adapted from the same sound files as Boot et al. (2005), which involved a digitized voice reading a string of 8 digits at a rate of 2 per second for 4 seconds. The eight digits were randomly generated from the

numbers one to nine, and each sequence was constrained to have one, two or three sequential repetitions. The sequence of numbers would start with the depression of the response button, and the onset of the target was randomised to appear between 1000 and 1500ms from the start of the number sequence. In the dual task condition, the participant was required to monitor the auditory string of digits for sequential repetitions and to report whether they had heard one, two or three pairs of numbers in the sequence. The participants were required to touch the appropriate numbered button on the touch-screen to record their response, which was presented at the end of each trial. On any trial in which the participant made an incorrect response for the number of sequential repetitions, the participant received feedback via a low error tone, and the trial was recycled to the end of the block with a novel digit string. In the single task condition, the auditory string of digits was to be ignored and an 'OK' button needed to be pressed to continue with the next trial.

Before the experimental blocks of trials, the participant received a practice block of 30 unperturbed trials with two tones used to pace the participant's movements. The first tone was sounded 350ms after the start button was released and participants were instructed to touch the dot on the screen in time with the beep. The stimulus dot was removed from the screen at the time of the first beep, at 350ms. The second tone was sounded 1000ms after the start of the movement and participants were instructed to return to the start button after the second beep. In the experimental trials, there was no beep, as it might interfere with the auditory monitoring task, and participants were required to keep their finger on the screen until the 'OK' button (single task) or the 'How many pairs?' dialog box (dual task) appeared.

Apparatus

The apparatus used in Experiment 3 is identical to that previously described in Experiment 1. In addition, the auditory 1-back task was played at a clearly audible volume through speakers.

Procedure

Participants were required to complete a practice block of trials, to get them used to the required movement speed. As the experiment included an auditory task, it was deemed unsuitable to have a pacing beep. For the practice trials block, the participants were told that when they pushed down on the response button, a dot would appear on the screen. The participants were told that their job was to touch the dot on the screen in time with the first beep and hold their finger there until they heard the second beep. They should then bring their finger back to the button and press down to initiate the next trial.

In the experimental blocks, the participants were told that the task was essentially the same, but this time the dot would jump on some trials. The participants were also told that there would be numbers playing and in the single task condition they were to ignore the numbers and continue with the pointing task. At the end of the pointing movement, they were required to respond by pressing 'ok' to move onto the next trial. In the dual task condition, the participants were told that they needed to listen to the string of numbers and keep track of how many sequential repetitions of numbers were presented. At the end of the pointing movement, they were required to respond by touching the appropriate number displayed on the screen.

The further instructions differed for each condition, as detailed in Experiment 1.

Experiment 3: Results

Auditory Task

The reaching trials in which participants made an error in auditory 1-back task were excluded and recycled. In order to collect 100 trials with correct 1-back performance, each participant completed an average of 127 trials (SD: 11.81) in the dual task condition, resulting in a 21.3% error rate for the secondary task. This level of performance confirms that the auditory 1-back task was cognitively demanding.

A mixed-model ANOVA was performed on arcsine-transformed percentage error rates, to examine the influence of condition (GO, STOP, NOGO) and perturbation (unperturbed, perturbed). The main effect of perturbation was significant, with higher error rates on perturbed trials (24.9%, SD 1.0) than on unperturbed trials (18.5%, SD 7.0) [$F(1,21) = 48.37$, $p < 0.000$]. This effect interacted significantly with condition [$F(1,21) = 3.85$, $p < 0.05$], as the increase of error rate in the perturbed trials was greater under the STOP instruction (10.2%, SD 6.4) than under GO (4.7%, SD 3.7) or NOGO (4.6%, SD 2.8) instructions. The differentially greater interference on the perturbed trials under the STOP instruction is consistent with an increased cognitive load associated with the voluntary stop response. Importantly, the main effect of condition did not approach significance [$p = 0.56$], indicating that comparable cognitive resources were allocated to the auditory task across instruction conditions.

Reaching Task: Unperturbed Trials

The descriptive data from the unperturbed trials is summarised in Table 7.

Task	Condition	T2 position	RT	MT	PV	TPV	AE
Single Task	GO	Left	381.1 (129.4)	389.1 (26.1)	2441.4 (206.6)	100.9 (18.9)	0.2 (0.2)
		Right	378.2 (120.6)	377.2 (30.9)	2555.5 (260.3)	95.9 (15.5)	-0.1 (0.3)
	NOGO	Left	345.8 (53.5)	405.6 (54.3)	2267.0 (252.8)	111.9 (21.2)	0.2 (0.2)
		Right	347.9 (58.2)	389.4 (49.1)	2336.7 (259.6)	109.4 (21.6)	0.2 (0.2)
	STOP	Left	338.6 (54.6)	420.9 (35.9)	2376.4 (357.6)	106.3 (29.8)	0.2 (0.3)
		Right	339.9 (52.9)	407.2 (41.5)	2452.4 (393.9)	102.8 (32.2)	0.1 (0.1)
Dual Task	GO	Left	413.9 (53.9)	390.3 (32.0)	2483.2 (269.5)	100.0 (11.9)	0.1 (0.1)
		Right	409.0 (39.9)	377.5 (31.6)	2582.2 (241.2)	98.1 (13.1)	-0.1 (0.2)
	NOGO	Left	496.4 (176.7)	386.6 (36.6)	2264.4 (95.5)	111.9 (19.5)	0.1 (0.2)
		Right	456.8 (118.7)	384.7 (39.2)	2319.1 (93.9)	112.2 (18.9)	0.3 (0.3)
	STOP	Left	465.2 (101.5)	415.0 (27.4)	2431.8 (298.2)	110.6 (23.7)	0.2 (0.3)
		Right	431.3 (68.2)	406.6 (29.1)	2490.2 (295.9)	110.9 (18.9)	0.2 (0.2)

Table 7: Means for the unperturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets).

A mixed-model analysis of variance (ANOVA) separately RT, MT, PV, TPV and AE with task (single, dual) and side of presentation (left, right) as within subjects factors, and condition (GO, STOP, NOGO) as a between subjects factor.

There was no main effect of condition for any of the dependent variables [$p \geq 0.154$], which suggests that the participants were behaving in an equivalent manner in all three conditions. For RT, there was a main effect of task [$F(1,21) = 21.141$; $p<0.001$], with participants taking on average 90 ms longer to initiate their movement in the dual task, but not for any of the other movement characteristics [MT, PV, TPV and AE, $p \geq 0.358$]. Reaction times were slower for left sided targets [$F(1,21) = 6.741$; $p<0.05$], especially in the dual task, with a significant task x side of presentation interaction [$F(1,21) = 5.906$; $p<0.05$].

Movement times were also longer for targets on the left [$F(1,21) = 32.656$; $p<0.001$] and a slower peak velocity was reached for left-sided targets [$F(1,21) = 27.514$; $p=0.000$], than for right-sided targets. Although there was not a statistically reliable effect of the side of presentation on TPV or the AE of the movement [both $p\geq0.080$], this could be due to the small difference in the distance (27mm either side of the midline) between the left and right target presentation locations.

Reaching Task: Perturbed Trails

Condition	Task	Target jump Left to Right	Target jump Right to Left
GO	Single	96.2	93.7
	Dual	97.5	96.6
NOGO	Single	0.8	2.5
	Dual	5.2	5.2
STOP	Single	81.0	79.3
	Dual	94.2	86.1
Corrected but not stopped	Single	4.2	6.8
	Dual	7.2	4.5

Table 8: The percentages of perturbed trials corrected towards the new target location for each of the three conditions in the single and dual tasks. The 'corrected but not stopped' row refers to those trials in the STOP condition during which the participant modified their trajectory towards the target but was unable to stop their movement before touching the screen

As can be seen from Table 8, there is a low percentage of corrected trials in the NOGO condition. In the single task trials, four participants did not correct on any perturbed trials and the other four only corrected towards the direction of the jump on one trial. Under dual task conditions, three participants did not correct on any trial and two only corrected once, with the other participants correcting on no more than two trials each for either direction of the target jump. These counts are too low to include the NOGO condition in an analysis of corrected

trials. As can be seen from Table 1, and as in Experiment 1, there was also an under representation of corrected but not stopped trials in the STOP condition. In both the single and the dual tasks, three participants did not produce any failures to stop in reaction to the target perturbation, and the other participants were unable to stop their movements on no more than three trials on either side. As explained previously, it would not be sensible to compare the perturbed corrected GO trials and the successfully stopped trials in the STOP condition, as they are not equivalent movements, therefore the following analysis is performed separately for the GO and STOP conditions.

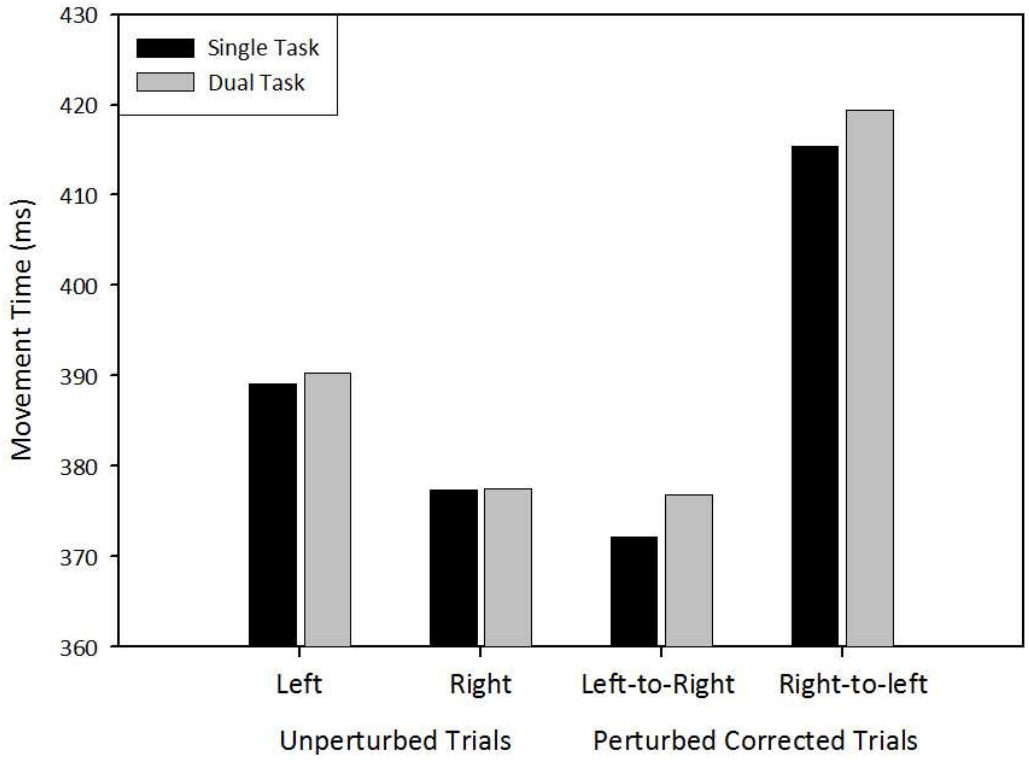
GO Condition

A 2 (task: single, dual) x 2 (position of T1: left, right) x 2 (perturbation: unperturbed, perturbed corrected) repeated-measures ANOVA was performed separately on MT, PV, TPV and AE.

For all of the variables, there was no main effect of task [$p \geq 0.180$], and so being under dual task conditions performing a concurrent auditory 1-back task did not have a significant effect upon the MT, PV, TPV or the AE of the movement in the pointing task. There was a main effect of T1 position with higher peak velocities [$F(1,7) = 47.912$; $p < 0.001$] for targets located on the right, but there was no reliable difference between the unperturbed and corrected perturbed trials in the peak velocity reached or the time taken to reach peak velocity [$p \geq 0.483$].

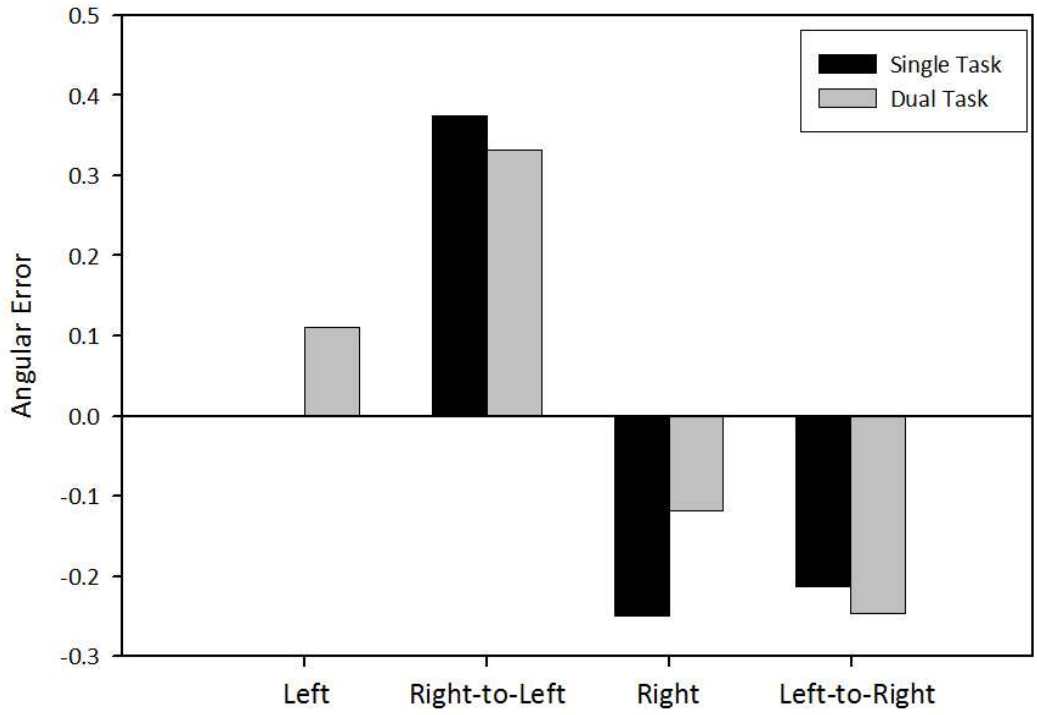
There was a main effect of T1 position [$F(1,7) = 8.715$; $p < 0.05$] and a main effect of perturbation [$F(1,7) = 11.089$; $p < 0.05$] on MT, but these were driven by a highly significant interaction [$F(1,7) = 24.022$; $p < 0.005$], with longer movement times for perturbed trials with the target jumping from right-to-left, as illustrated in Figure 7.

Figure 7: The movement times plotted in milliseconds for the unperturbed and perturbed corrected trials in the GO condition



There was also a significant direction of jump x perturbation interaction for AE [$F(1,7) = 13.395$; $p<0.01$], with larger errors for targets jumping right-to-left. As in Experiment 1, there are no errors in the unperturbed left-sided trials in the single task, and a greater degree of rightward errors for perturbed targets presented on the right and jumping to the left overall (Figure 8). The corrections towards a rightwards jumping target could be considered 'complete', as the errors are similar to the unperturbed trials during which the target was presented, and remained, on the right. The corrections towards leftwards target jumps however, are incomplete, with more rightward error than when reaching towards the stationary left target position.

Figure 8: The directional angular error for the unperturbed and perturbed trials in the GO condition.



A further 2 (task: single, dual) x 2 (direction of target jump: left, right) repeated-measures ANOVA was performed using the perturbed corrected trials on CT. The CT analysis revealed a main effect of direction of target jump [$F(1,7) = 32.838$; $p \leq 0.001$], with the hand taking longer to arrive in a spatially corrected position for targets that jumped from right-to-left, supporting the findings from Experiment 1. In addition, there was also a main effect of task [$(1,7) = 15.920$; $p \leq 0.005$], with corrections made under single task conditions taking longer to become evident on the spatial analysis. The results of the CT analysis do not mean that corrections towards targets jumping from right-to-left are implemented later than the corrections towards rightward perturbed targets, and that all corrections in the single task take longer to occur than in the dual task, only that these corrections take longer to lead to a significant change in hand path, as determined by the spatial algorithm. This could be due to a longer

latency, or a reduced vigour of correction (see the horizontal acceleration analysis for a temporal explanation and further discussion).

STOP Condition

A 2 (task: single, dual) x 2 (direction of target jump: left, right) repeated-measures ANOVA was performed using perturbed corrected trials on CT, stop time (movement time up to the point of backwards velocity, as the hand is pulled back) and stop rate (the proportion of successful STOP responses).

There was no main effect of task for CT [$p=0.230$], nor was there a significant effect of direction of target jump [$p=0.126$]. As can be seen in Table 9, there is however, a trend for movements towards targets jumping from right-to-left to have longer correction times, as was the case in Experiment 1. The reasoning put forward was that corrections in the STOP condition were not as vigorous as those in the GO condition, and as can be seen in Figures 10 to 12, this explanation is also fitting for the findings in this study. The more muted corrections in the STOP condition, as demonstrated in the horizontal acceleration analysis below, would not be so rapidly or reliably detected on a spatial analysis such as CT, because the hand would take longer to arrive in a corrected position, and might not escape the bandwidth of unperturbed trials before the end of the movement on some occasions, even if a correction had in fact been initiated.

There was no main effect of task [$p\geq0.454$] or direction of the target jump [$p\geq0.171$] for stop time or stop rate. There were however statistically reliable interactions for both STOP time and STOP rate, with longer stop times for targets jumping right to left in the dual condition [$F(1,7) = 8.763$; $p<0.05$] and a higher proportion of successful stops for targets jumping left-to-right in the single condition and for targets jumping right-to-left in the dual condition [$F(1,7) = 7.540$; $p<0.05$].

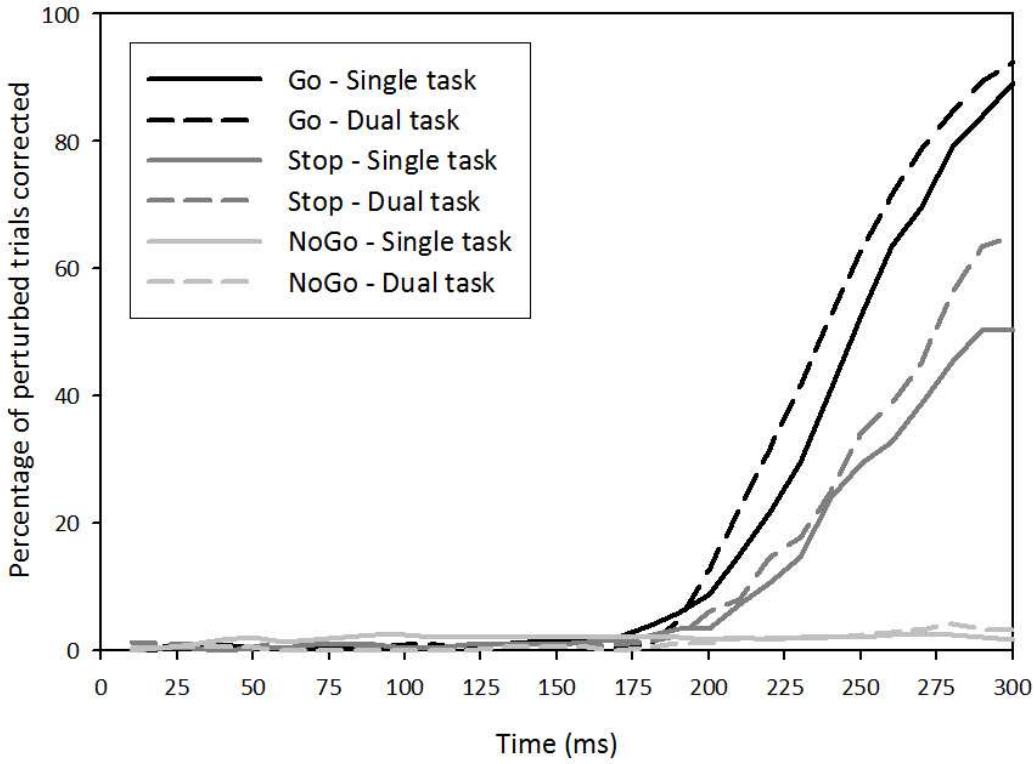
	Task	Left to Right	Right to Left
Correction time	Single	244.8 (56.8)	266.3 (43.6)
	Dual	239.4 (46.8)	267.2 (41.4)
Stop time	Single	340.0 (56.5)	345.3 (68.1)
	Dual	339.7 (53.1)	355.2 (67.4)
Stop rate	Single	94.8%	94.5%
	Dual	92.4%	94.8%

Table 9: Mean correction time and mean stop time in corrected and stopped perturbed trials (ms) and percentage stop rate in corrected perturbed trials.(Standard deviations given in brackets).

Individual Corrections

As can be seen in Figure 9, The GO condition resulted in a much higher rate of corrections than the STOP condition, and correction rate in the NOGO condition was very low, with only 2.5% corrections under single task conditions and 4.1% corrections made towards perturbed targets in the dual task situation. It is also observable that the dual task situation produced more corrections than the single task. One explanation could be that the dual task conditions may have increased arousal and this in turn may have focused concentration on the pointing task and led to higher rates of corrections. Participants in the GO condition also appear to begin to correct slightly earlier in their movements than those in the STOP condition. This observation is not statistically supported (see CT analysis above), but conforms to the general pattern, with the finding of greater amplitude of corrections in the GO condition, as discussed in horizontal acceleration analysis below.

Figure 9: The mean rates of individual bilateral current corrections for the GO, STOP and NOGO conditions for both the single and dual tasks. The Single task trials are plotted in solid lines and the Dual task trials are plotted in dashed lines.



A mixed-model ANOVA was performed on the rate of individual corrections at each 10ms interval from 0 to 300ms (30 levels), with task (single, dual) and direction of target jump (left, right) as within subjects factors and condition (GO, STOP, NOGO) as a between subjects factor. The analysis was cut off at 300ms because the majority of participants in the STOP condition produced movements that did not last longer then 300ms, and by 350ms, there was only one STOP condition participant and five NOGO participants contributing to the analysis.

At 210ms, the effect of condition becomes reliable [$p \leq 0.022$], with the GO and NOGO conditions significantly different from each other and by 240ms, all of the conditions are significantly different from each other [$p \leq 0.046$]. From 200ms

there is a main effect of direction of target jump, with more corrections for targets jumping from left-to-right than right-to-left [p≤ 0.028] and between 210ms and 250 ms there is also a main effect of task, with more corrections in the dual task [p≤ 0.046].

Horizontal Acceleration Profiles

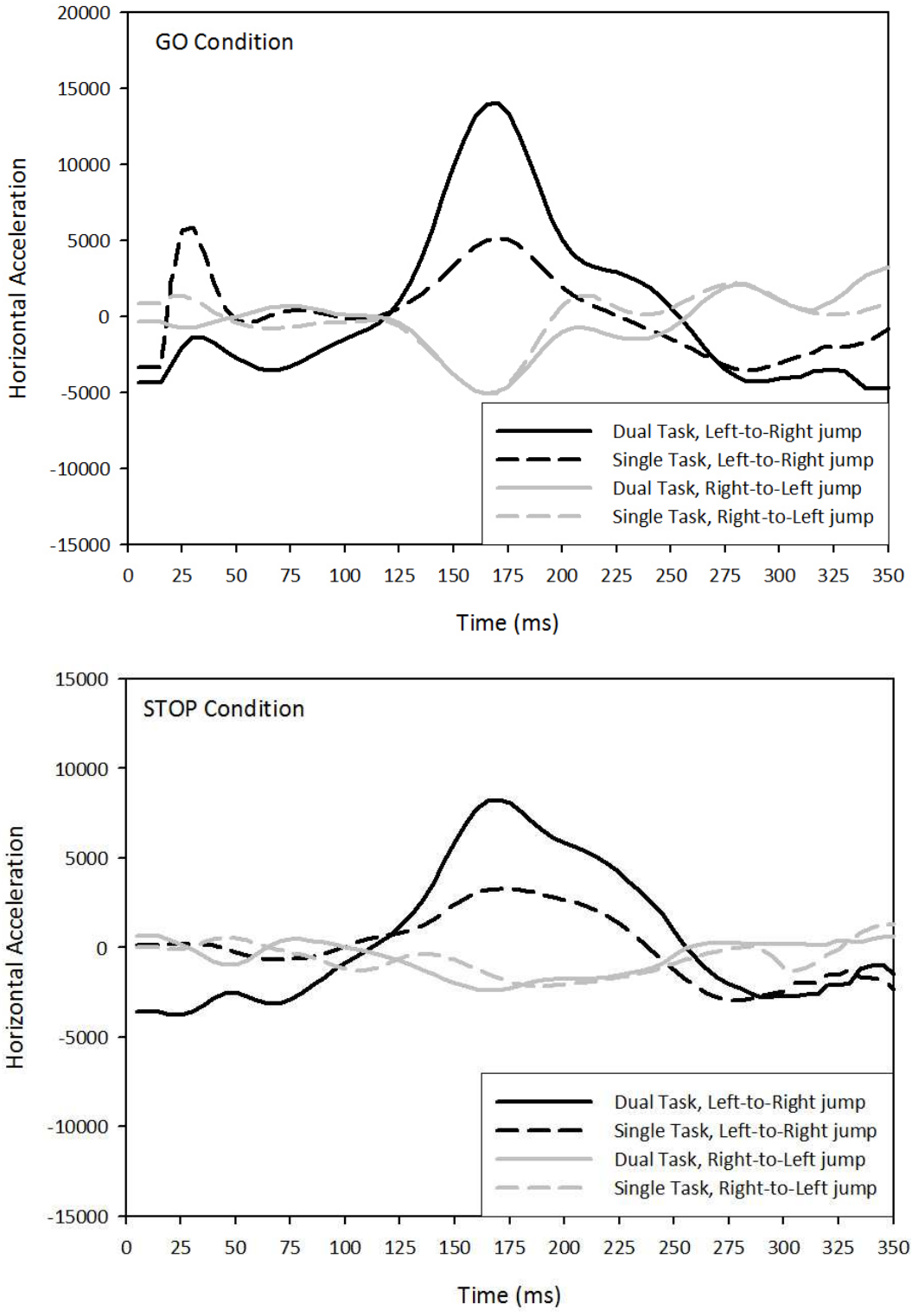
As in the perturbed analysis, the number of corrected perturbed trials was too low in the NOGO condition to be included in the analysis (see Table 8), with the maximum corrected perturbed trials contributed by any participant being one in the single task and two in the dual task. Therefore, the analysis of the horizontal acceleration profile contains trials from the GO and STOP conditions only.

Single Task

A repeated-measures ANOVA was performed on horizontal acceleration with condition (GO, STOP) as a within subjects factor and perturbation (baseline, perturbed corrected) as the between subjects factor. In order for any effect to be considered, it had to remain significant for 50ms.

For targets that jumped from left to right, corrections occurred at 140ms [p≤ 0.022] (see Figure 10), with corrections occurring slightly earlier in the STOP condition. The rightwards acceleration was greater in the GO condition than in the STOP condition. Corrections are occurring slightly later for jumps from right-to-left, starting at 145ms [p≤ 0.042], as can be seen in Figure 10. Again, as with the left-to-right jumps, the amplitude of the reacceleration for the corrections is greater in the GO condition than in the STOP condition.

Figure 10: The mean horizontal acceleration profiles for left and right perturbed trials, computed as a difference from baseline, for movements under the GO and STOP condition instructions in the Single and Dual task.



Dual Task

A repeated-measures ANOVA was performed on horizontal acceleration with condition (GO, STOP) as a within subjects factor and perturbation (baseline, perturbed corrected) as the between subjects factor. Again, in order for any effect to be considered, it had to remain significant for 50ms

As Figure 10 shows, corrections for jumps from left-to-right are starting at 135ms [$p \leq 0.048$]. As in all the other comparisons, the GO instruction resulted in a greater amplitude of correction, than the instruction to STOP the movement and pull the hand back to the start position.

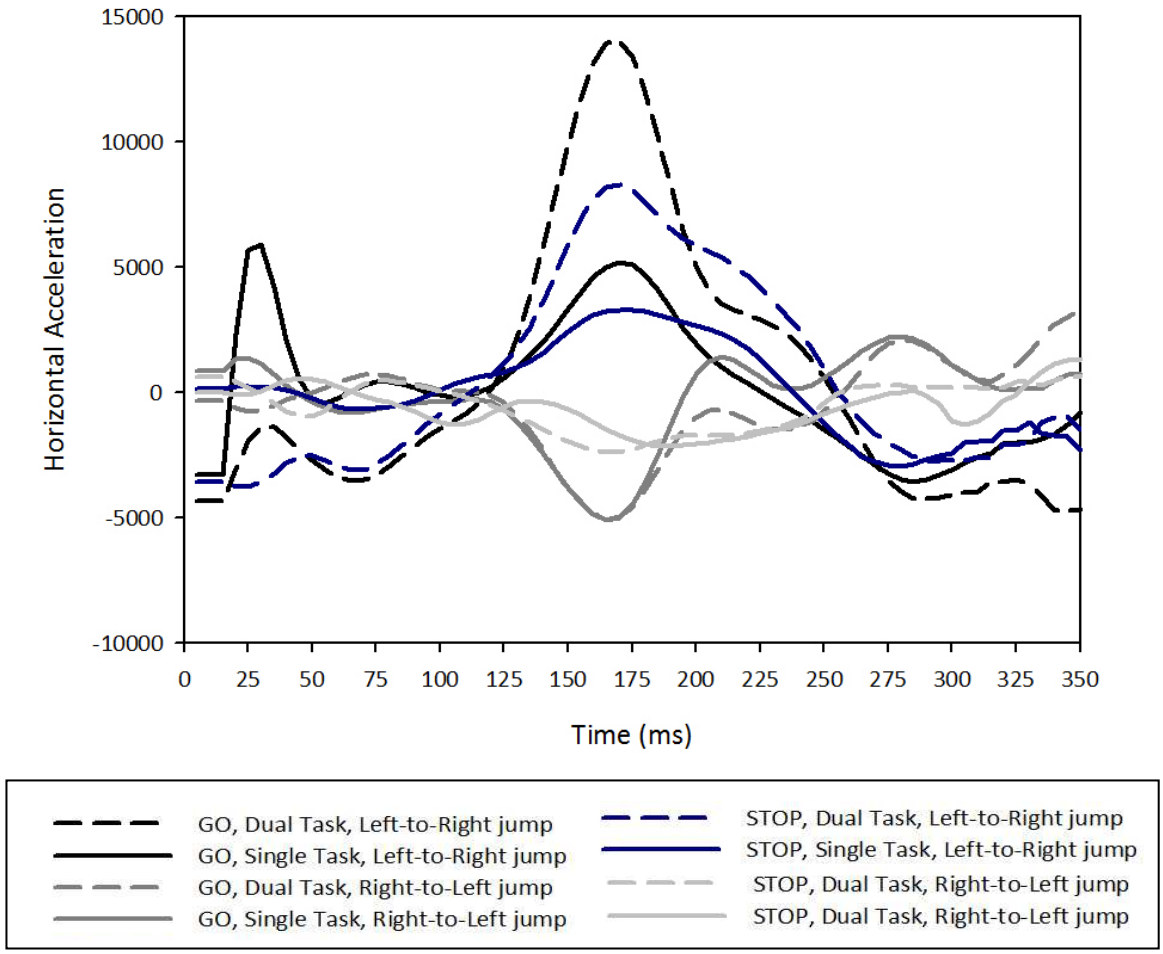
In contrast to the trend in Experiment 1 and in the single task, corrections to jumps from right-to-left occur slightly earlier than left-to-right during the dual task, at 125ms, for both the GO and STOP conditions [$p \leq 0.037$]. However, the greater amplitude of corrections in the GO condition than in the STOP condition is still observable.

Single and Dual tasks

When directly comparing the corrections to left-to-right and right-to-left perturbed trials (computed as a difference from baseline) in a 2 (condition: GO, STOP) x 2 (task: single, dual) x 2 (direction of target jump: left, right) mixed-model ANOVA, there was a significant difference between corrections to the left and right starting at 140ms [$p \leq 0.033$], with earlier corrections towards targets jumping from left-to-right (see Figure 11). The latency of the corrections was the same for targets jumping to the left and the right, but the amplitude of the acceleration was larger for targets jumping from left-to-right. This was why the CT analysis detected the corrections for right-to-left perturbations later than for left-to-right perturbations, because the amplitude of the correction was not as strong. The corrections were made earlier in the dual task at 135ms [$p \leq 0.048$], but mainly in the left-to-right perturbations (direction of target jump x task

interaction starting at 140ms; p≤ 0.046). This also confirms to the CT analysis, with the corrections made under the dual task conditions showing up earlier on the spatial analysis, due to the greater vigour of the corrections being made.

Figure 11: The horizontal acceleration profile for perturbation trials (computed as a difference from baseline), for targets jumping left-to-right and right-to-left in GO and STOP conditions and single and dual tasks



The difference in the corrections between the GO and the STOP conditions is the strength of the correction. Figure 11 demonstrates the difference between the GO and the STOP conditions, with higher peaks for the GO condition. This is especially evident for the trials in which the target was perturbed from left-to-right, with greater acceleration in the rightwards direction, than the leftwards

acceleration for targets jumping right-to-left, replicating the findings of Experiment 1. The horizontal acceleration analysis suggests that the corrections are initiated at a similar time, but the corrections in the GO condition are more vigorous (and more frequent). As observed in Experiment 1, the conscious intention to make corrections facilitates this behaviour and results in corrections that are more forceful and more frequent in comparison with the uninstructed automatic corrections in the STOP condition. In addition, there is a striking difference in the amount of vigour applied to the correction under the Dual task conditions, in comparison to the Single task trials, as can be seen in the dotted lines of Figure 11.

Summary

The results of Experiment 3 replicate those in Experiment 1. The rates of corrections produced in the GO, STOP and NOGO conditions were similar to those in the earlier experiments, and the rightwards bias is also evident. The conscious intention to make the corrections in the GO condition does not affect the timing, but does affect the strength of the correction towards the target perturbation, with a higher peak of horizontal acceleration evident in Figures 10 and 11 for the GO condition.

Evidence from the individual corrections analysis and the horizontal acceleration analysis, backed up by the CT analysis, suggests that the dual task situation appears to enhance this behaviour even further. Figure 11 shows the higher amplitude of corrections made in the dual task in both conditions and Figure 9 demonstrates the higher rates of corrections made under the dual task conditions. In an attempt to reduce the conscious processes available for the pointing task, by using the concurrent auditory 1-back task, the level of arousal and concentration may have actually been raised, rather than the level of available cognitive resources reduced. On the whole, being under the added pressure of the dual task situation may have forced participants to concentrate

harder, which in the case of the GO condition, resulted in even more corrections towards perturbations than in the single task, and so appears to have facilitated the facilitation effects of conscious intention.

Experiment 3: Discussion

Experiment 3 set out to investigate the effect of a dual task situation on the ability to produce online corrections in a double-step task. The hypothesis for this experiment was that correction rates in the GO condition would decrease and correction rates in the NOGO condition would increase in the dual task block, in comparison with the single task block. A further hypothesis was that the STOP response may reveal the default rate of correction and would therefore not be affected by concurrently performing the 1-back task. As can be seen from Figure 9, this hypothesis was not supported by the data collected. For the GO and the STOP conditions, the additional auditory task actually increased the number of corrections produced and led to improved correction efficiency, in comparison to the single task trials.

Encouragingly, the performance observed in the current experiment in the single task trials, replicates the pattern of results found in Experiment 1. High rates of correction were produced for the GO condition, moderate rates were produced in the STOP condition, and low rates of correction were produced in the NOGO correction, with the rightwards target bias also present. Again, the rates of correction were greater and the movement kinematics reveal quicker, more accurate movements towards targets presented on, or jumping towards, the right.

With equivalent performance in the single task to that in previous experiments, the focus of this discussion must be on the dual task performance, and the dual

task itself. The first place to start would be to examine the choice of dual task. The findings from Boot et al. (2005) suggest that the n-back task is an adequate task to use as a secondary task. In their study, the n-back was used as a secondary task in an attentional capture paradigm, with the auditory task having a significant effect on the ability to attend to abrupt onsets. During the single task condition, when participants were instructed to ignore the auditory stream of digits, abrupt onsets captured attention. However, in the dual task, when participants were required to monitor the digit string for repetitions, onsets failed to capture attention (Boot et al. 2005).

The n-back task has also been used successfully as a working memory load in studies looking at traumatic brain injury (McAllister, Sparling, Flashman, Guerin, Mamourian, & Saykin, 2001; Perlstein et al. 2004). In these studies, the n-back was made up of strings of consonant letters, and the working memory load was manipulated by using 0-, 1-, 2- and 3-back tasks. Perlstein et al. (2004) describe the n-back task, as a task that 'requires monitoring and coding of incoming information, maintaining the appropriate number of items in a "buffer," temporally tagging, sequencing and updating the information held in the buffer, and replacing no-longer relevant information with newer, more relevant information.' (pg. 725) This statement, along with the findings in the wider literature, suggests that the choice of secondary task in the current experiment was an appropriate task to use in this instance.

An alternative explanation for the lack of dual task interference is that it may have been possible for participants to synchronise their manual aiming movements with a gap in the digit string and therefore use attentional switching to complete the task successfully. The aiming movement takes 300-350ms to complete and the numbers in the n-back task were presented one every 500ms, so this tactic could possibly have been used. However, one would expect a task switching cost to be observable as a detriment in the task performance (Jersild, 1927), yet the performance on the manual pointing task was actually improved.

It is therefore possible to reject task switching as an explanation of the findings. Thus, any proposals that the secondary task is tapping the wrong resources, may not be hard enough, or may not place an adequately heavy load on conscious resources do not seem applicable to the n-back task, which has successfully be used in a number of previous studies.

If the lack of the hypothesised dual task effect cannot be attributed to the choice of dual task, then maybe it can be attributed to the automatic pilot itself. One possible explanation is that the automatic pilot has different settings, much like the attentional set discussed in more detail in the next chapter. The attentional set is a term from the visual attention literature which describes how cognitive goals, as determined by the task instructions influence the successful completion of a task. If the task requires you to find a red square amongst green squares, then your attentional set is set offline to 'red square', and then any stimulus that matches the setting will capture attention online, without the need for conscious involvement (Folk Remington & Johnston, 1992). The attentional set would be guided by the task instructions and can be set so rigidly that objects that would otherwise be highly salient are not attended to, when they are irrelevant to the task (Theeuwes, 1991; Yantis & Jonides, 1990). The same kind of attentional setting could be evident in the automatic pilot. Once the GO, STOP, or NOGO instruction has been administered, and the cognitive goals 'set', then the system does not require any further cognitive effort for that setting to be maintained. Therefore in the current experiment in the dual task trials, the participants received their manual aiming task instructions, set their automatic pilot, and then continued with the n-back task, without having to continually sustain the GO, STOP or NOGO instruction.

In addition, not only were the task instructions maintained throughout the dual task trials, the performance during these trials was enhanced in comparison to the single task performance for the GO and STOP conditions. One potential explanation for this is that the dual task environment led to increased arousal

and therefore increased performance on the manual aiming task. The n-back task is demanding, as discussed earlier, and so may have forced participants to concentrate harder on both tasks, leading to the heightened performance. Furthermore, the rates of correction produced in Experiment 3 were close to ceiling, as several participants achieved maximal (or near-maximal) rates of correction in the GO task, and minimal (or near-minimal) rates in the NOGO task, and so any detrimental effect of the dual task on correction performance would be difficult to observe. In order to provide a more definitive test of the cognitive load criterion of automaticity, it would be necessary to induce sub-ceiling levels of performance in the single-task.

The increased performance under the dual task conditions was not expected, and as discussed, could have been due to a number of potential factors. In order to resolve the secondary task issue, it is necessary to conduct a further experiment. The next experiment will attempt to make the manual aiming task more difficult, by requiring participants to switch between GO and NOGO instructions, whilst maintaining their performance on the same 1-back task, potentially providing a validation of the 1-back task as the choice of secondary task, and in an attempt to reduce the ceiling performance in the single task.

Experiment 4: Introduction

One explanation for the surprising results in Experiment 3 was that the automatic pilot may be capable of operating in different modes, according to the high-level attentional set adopted by the person, and manipulated by the task instruction in the present experiments. It appears from Experiment 3 that once the instruction has been given, and the required response taken on board, then it may not require cognitive effort to maintain that instructed response set.

The maintenance of the response set may have been assisted by the fact that the participants recruited for the research were naïve to the experiment and were required to perform the task under only one between-subjects instruction condition. For example, the GO participants knew about the GO instructions only, and NOGO participants knew about the NOGO instruction only, and this may have made the attentional set easier, or less cognitively demanding, to maintain. Experiment 4 set out to increase the difficulty of maintaining the required attentional set, by requiring participants to switch between the GO and the NOGO instructions whilst simultaneously performing the 1-back task.

The hypothesis for Experiment 4 remains the same as for Experiment 3, with the STOP response correction level being the default level and the GO and NOGO correction rates being the result of conscious intention. It is expected that there will be observable switch costs in performance, with the GO rates of correction lower, and the NOGO rates higher, than in Experiment 3. The main interest however, in Experiment 4, is whether these switch costs are symmetrically or asymmetrically expressed for the two types of switches, as this will identify which of the attentional states the automatic pilot system prefers to occupy. It would be expected that if the GO condition is more difficult to maintain, then the correction rates would fall in the dual task trials, and if the NOGO condition is harder to maintain, then the rates of correction would increase during the dual task trials, as the automatic pilot reverts to the default level when under heavy cognitive load. However, it is hypothesised that the GO condition would be the favoured setting of the automatic pilot, as it seems more natural, considering both the demands of everyday life, and given the introspective experience of performing the different tasks. Indeed, several participants in the various NOGO conditions commented informally that the NOGO task felt ‘difficult’ or ‘unnatural’.

Experiment 4: Methods

Participants

Sixteen naïve adult volunteers (9 females and 6 males, mean age: 22.18 years, SD: 4.04) took part in the study. The participants were recruited using the same procedure as detailed in Experiment 1. All of the participants were right-handed and reported no visual or motor deficits.

Design

The study consisted of two within-subjects conditions, the GO condition and the NOGO condition. The two conditions were intermixed, with the task instruction alternated every 20 trials. Participants performed 200 trials of each condition, 100 trials performed under single task conditions and 100 trials under dual task conditions, counterbalanced amongst participants. The experiment was conducted in four blocks of 100 trials, and each 100 trial block was made up of five mini-blocks of 20 trials. The GO dominant and NOGO dominant trial orders were counterbalanced across participants.

As in Experiment 3, there was a 30% perturbation rate, with the target jumping to the left or right an equal number of times. On the further 70% of trials, the target remained stationary when the participant released the button, and on all trials, the target was presented on the right in 50% of the trials and on the left in the other 50% of trials. Two differences between the current experiment and Experiment 3, are that the trials were presented in a fixed (pseudo-randomised) order and trials with an associated incorrect n-back performance were not recycled. Breaks were given to the participants after every 100 trials, and eight calibration trials were recorded at the end of the fourth block. Across all trials (single and dual task) there was a concurrent auditory 1-back stimulus train presented (Boot et al., 2005), as detailed in Experiment 3. Participants were

instructed to monitor the stream for sequential repetitions in the dual-task condition, and simply to ignore the auditory stimulus in the dual task condition.

Before the experimental blocks of trials, the participant received a practice block of 10 trials in the GO condition and 10 trials in the NOGO condition, with a 30% perturbation rate. This was in order for participants to experience the task switching nature of the experiment, and to ensure understanding of the task instructions.

Apparatus

The apparatus used in this experiment is the same as detailed in Experiment 3. In addition, the stimulus dot now also provided a reminder of which task instruction the participant was to follow. In the GO trials, the stimulus dot appeared green when the participant pressed down the response button, and turned to white (the signal to move) at a variable time interval between 1000 and 1500 ms after the button was depressed. In the NOGO trials, the dot was red at the beginning of the trial. In addition to the colour cue, which appeared on every trial, a written instruction appeared in the centre of the screen at the beginning of each 20 trial mini-block, instructing the participant either to follow or to not follow the target.

Procedure

The task was explained to participants, firstly by introducing the unperturbed trials, and then by describing the two perturbed conditions. The practice block was then performed, which enabled the experimenter to check that the task instructions were understood. The task instructions for the GO and NOGO trials are described in Experiment 1, with the single and dual task instructions detailed in Experiment 3.

Participants were instructed to switch between the two instructions depending on the written instruction and the coloured dot reminder, and when in the dual task blocks to concurrently perform the 1-back task.

Experiment 4: Results

Auditory Task

Error rates in the auditory 1-back task were higher overall than those in Experiment 3 (GO 29.2%, NOGO 30.6%), consistent with the greater cognitive demand imposed by the changing reach instruction. A mixed-model ANOVA was performed on arcsine-transformed percentage error rates, to examine the influence of condition (GO, NOGO) and perturbation (unperturbed, perturbed). No effects approached significance [$p \geq 0.17$]. Unlike in Experiment 3, then, the target jump did not interfere with performance of the auditory task; the distracting influence of the jump may have been masked by the overall greater cognitive demand in the current experiment. As in Experiment 3, the lack of main effect of condition indicates that comparable cognitive resources were allocated to the auditory task across instruction conditions. Unlike in Experiment 3, reaching trials with errors in the auditory task were not excluded, since ~30% of observations would have been lost; however, exploratory analyses performed without these trials gave similar results.

Reaching Task: Unperturbed Trials

A 2 (task: single, dual) x 2 (condition: GO, NOGO) x 2 (target 2 location: left, right) repeated measures ANOVA was performed separately on RT, MT, PV, TPV and AE for the unperturbed trials.

There was an effect of task on the reaction times to targets in the unperturbed trials, with faster reaction times in the single task condition [$F(1,15) = 48.60$; $p<0.001$], compared to the dual task condition, and a significant effect of condition [$F(1,15) = 43.34$; $p<0.001$], with faster reaction times in the NOGO condition. Faster reaction times in the NOGO condition can perhaps be explained by the fact that the instructions require participants to aim for the original location of the target if the target jumps, and although this analysis is restricted to the unperturbed trials, the reduced unpredictability in the NOGO condition is reflected in the faster reaction times.

In terms of the movement kinematics, there was no main effect of task or condition on the movement times, the peak velocity reached or the time to reach peak velocity. There was however, a statistically reliable effect of the target location, with shorter movement times [$F(1,15) = 57.85$; $p<0.001$], higher peak velocities reached [$F(1,15) = 98.49$; $p<0.001$], and shorter times to reach peak velocity [$F(1,15) = 4.67$; $p<0.05$] for targets presented on the right. These results are accompanied by two significant task x target 2 location interactions, with shorter movement times towards targets on the right in the dual task [$F(1,15) = 5.47$; $p<0.05$] and shorter times to reach peak velocity towards targets on the right on the single task [$F(1,15) = 7.69$; $p<0.05$].

The GO condition resulted in greater AE than the NOGO condition [$F(1,15) = 9.31$; $p<0.01$], and this could be explained by the uncertainty in the GO trial blocks, and the need to follow the target if it jumps. There are also significant interactions for task x condition [$F(1,15) = 4.49$; $p=0.051$] and condition x side [$F(1,15) = 14.53$; $p<0.005$], with more rightwards errors in the GO condition during the dual task and more rightwards errors in the GO condition for targets presented on the left.

Task	Condition	T2 position	RT	MT	PV	TPV	AE
Single Task	GO	Left	363.8 (63.1)	447.6 (88.8)	2093.4 (377.2)	132.1 (46.4)	0.3 (0.4)
		Right	350.7 (61.7)	440.0 (90.4)	2168.9 (409.4)	136.3 (49.5)	0.1 (0.4)
	NOGO	Left	317.6 (49.2)	445.0 (89.5)	2073.3 (371.9)	135.5 (46.9)	0.0 (0.4)
		Right	313.1 (52.4)	438.1 (90.2)	2176.3 (412.5)	133.7 (47.2)	0.2 (0.3)
Dual Task	GO	Left	430.1 (72.1)	459.7 (104.7)	2044.6 (374.8)	143.1 (49.7)	0.3 (0.4)
		Right	441.5 (113.0)	438.4 (92.3)	2149.2 (378.5)	138.5 (47.6)	0.2 (0.3)
	NOGO	Left	405.8 (83.9)	446.1 (92.4)	2092.6 (370.8)	140.0 (42.9)	0.0 (0.4)
		Right	379.0 (68.4)	430.9 (84.3)	2196.7 (359.8)	130.9 (37.6)	0.2 (0.4)

Table 10: Means for the unperturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets).

Reaching Task: Perturbed Trails

In the current experiment, there is a GO and a NOGO condition, and these conditions differ in the required behaviour for successful completion. The GO condition requires participants to follow the target if it jumps, and therefore correct movements towards the new target location, whereas the NOGO condition requires participants to point to the original location of the target if it jumps, and therefore *not* correct their movements to the new target location. Consequently, the performance of these conditions resulted in few uncorrected perturbed trials in the GO condition, and few corrected perturbed trials in the NOGO condition. Therefore, the analysis of the GO trials will include only the corrected perturbed trials, and the analysis of the NOGO trials will involve the uncorrected perturbed trials only. These analyses are reported separately.

Task	Condition	T2 position	RT	MT	PV	TPV	AE	Percent corrected
Single Task	GO	Left	360.0 (61.3)	437.3 (93.2)	2105.4 (372.3)	142.5 (58.1)	-0.2 (0.7)	88.9%
		Right	357.6 (73.2)	483.6 (79.9)	2161.6 (413.2)	131.9 (38.7)	0.4 (0.3)	91.0%
	NOGO	Left	318.8 (86.9)	426.6 (91.6)	2160.8 (324.1)	134.8 (58.1)	-1.4 (1.3)	16.5%
		Right	307.6 (134.1)	446.8 (89.8)	2221.9 (407.1)	113.3 (46.9)	1.9 (2.0)	25.3%
Dual Task	GO	Left	426.7 (85.9)	442.0 (95.5)	2097.9 (326.3)	149.3 (45.5)	-0.3 (0.8)	90.4%
		Right	433.2 (75.9)	487.5 (73.6)	2124.6 (370.0)	131.3 (32.3)	0.3 (0.4)	89.6%
	NOGO	Left	377.5 (112.8)	482.3 (85.3)	1954.7 (298.3)	161.3 (50.0)	-0.6 (1.6)	27.6%
		Right	393.2 (132.9)	519.5 (113.4)	1982.9 (417.9)	139.5 (46.3)	1.6 (1.5)	36.1%

Table 11: Means for the corrected perturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets). In addition, in the 'percent corrected' column, the percentage of corrected *perturbed* trials are presented.

GO Condition

A 2 (task: single, dual) x 2 (perturbation: unperturbed, perturbed corrected) x 2 (jump direction: left, right) repeated measures ANOVA was performed separately on RT, MT, PV, TPV and AE for the trials in the GO condition.

As with the unperturbed trials, there was an effect of task on the reaction times to targets in the GO condition trials, with faster reaction times in the single task condition [$F(1,15) = 36.82$; $p<0.001$], compared to the dual task condition. There was no effect of task on any of the other dependent variables.

The MT, PV, TPV and AE of the movement endpoints are all significantly affected by the direction of the second target position. Targets that were initially presented on the right of the midline resulted in longer movement times [$F(1,15) = 13.21$; $p<0.005$], with a higher peak velocity [$F(1,15) = 17.62$; $p\leq0.001$], and a shorter time to reach the peak velocity [$F(1,15) = 12.51$;

$p<0.005$], with less AE [$F(1,15) = 6.05$; $p<0.05$], in comparison with targets presented on the left.

The target perturbation resulted in longer movement times [$F(1,15) = 14.13$; $p<0.005$] and more endpoint error [$F(1,15) = 10.64$; $p\leq0.005$] than the unperturbed trials, and there was a significant perturbation x target 2 position interaction [$F(1,15) = 14.51$; $p<0.005$], with more error in the perturbed trials that jump from the right to the left. There was a further perturbation x target 2 position interaction for the time to reach peak velocity [$F(1,15) = 10.51$; $p\leq0.005$], with the quickest time also in the perturbed trials that jumped from the right to the left.

NOGO Condition

A 2 (task: single, dual) x 2 (perturbation: unperturbed, perturbed uncorrected) x 2 (target 2 location: left, right) repeated measures ANOVA was performed separately on RT, MT, PV, TPV and AE for the trials in the NOGO condition.

As with the GO condition, there was an effect of task on the reaction times to targets in the GO condition trials, with faster reaction times in the single task condition [$F(1,14) = 50.38$; $p<0.001$], compared to the dual task condition. There was no effect of task on any of the other dependent variables.

Also as with the GO condition, the perturbed trials are completed quicker than the unperturbed trials [$F(1,14) = 5.08$; $p<0.05$]. In addition, MT, PV, TPV, and AE of the movement endpoints are also all significantly affected by the direction of the second target position. The movements towards a target that is presented on the right reach a higher peak velocity [$F(1,14) = 72.59$; $p<0.001$], and reach it sooner [$F(1,14) = 5.10$; $p<0.05$]. In contrast to the GO condition though, the movement times towards a right-sided target are shorter in the NOGO condition [$F(1,14) = 11.77$; $p<0.005$], than towards a left-sided target.

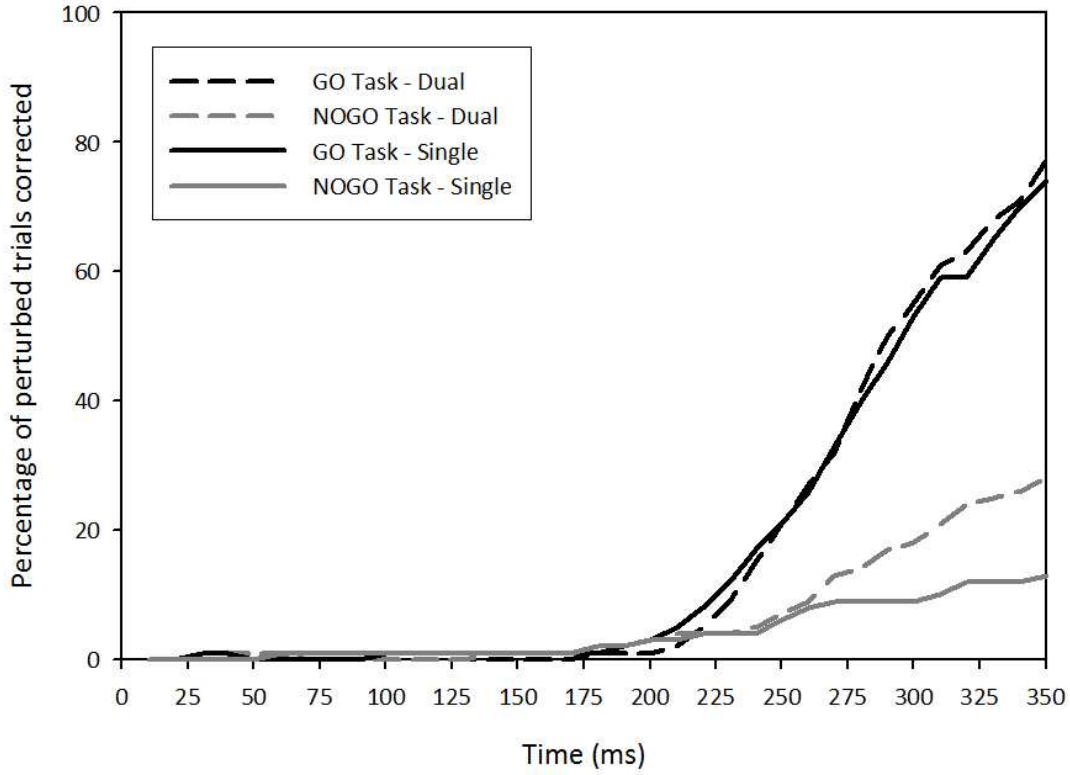
There was a significant three way interaction of task x perturbation x target 2 location [$F(1,14) = 7.49$; $p<0.05$] for the AE of the end points of the movements, demonstrating that movements towards perturbed targets with T2 on the left in the dual task were the least accurate. Movements under these conditions could be considered the most difficult, given the previous findings of the rightward bias. Biomechanically it would be more uncomfortable to reach into contralateral space, coupled with a target location perturbation and the additional cognitive load of the 1-back task.

Individual Corrections

The data for the individual corrections analysis was processed in the same way as described in the Methodology Chapter, except that the trials were grouped separately for each combination of condition (GO, NOGO) and task (single, dual). Thus, for example, perturbed trials in the GO-single condition were evaluated with respect to cut-offs derived from the unperturbed trials in the GO-single condition.

As can be seen from Figure 12, participants produce a higher percentage rate of corrections in the GO condition than when in the NOGO condition. It is also clear that the single and dual task environments did not affect the rate of corrections in the GO condition, but the dual task environment resulted in double the rate of corrections in the NOGO condition, in comparison to during the single task trials.

Figure 12: Mean bilateral individual corrections for the GO and NOGO conditions in the Single and Dual tasks. The GO condition is plotted in black and the NOGO condition is plotted in grey, with the Single task performance plotted in solid line and the Dual task performance indicated by the dashed lines.



A 2 (task: single, dual) x 2 (condition: GO, NOGO) x 2 (target 2 location: left, right) repeated measures ANOVA was performed on the rates of individual corrections for each 10ms time bin (35 levels).

There is a main effect of target 2 location from 200ms to 330ms [$p \leq 0.033$], with more corrections for targets that jump from left to right, and a main effect of condition from 230ms onwards [$p \leq 0.033$], with more corrections in the GO condition (as can be seen in Figure 12). There is no main effect of task, at any of the time bins, however there is a task x condition interaction from 320ms [$p \leq 0.049$], with an increase in corrections in the NOGO condition during the dual task.

Horizontal Acceleration Analysis

GO Condition

Analysing the horizontal acceleration profile, allows us to estimate the latency at which the correction towards the target perturbation occurred. In the current experiment, there were low numbers of corrected trials in the NOGO condition (see Table 11), and although the rates of corrected perturbed trials increased under the dual task, the number of corrected trials per participant is insufficient for this analysis. Therefore the horizontal acceleration analysis is restricted to the trials performed under the GO instruction in both the single and dual tasks.

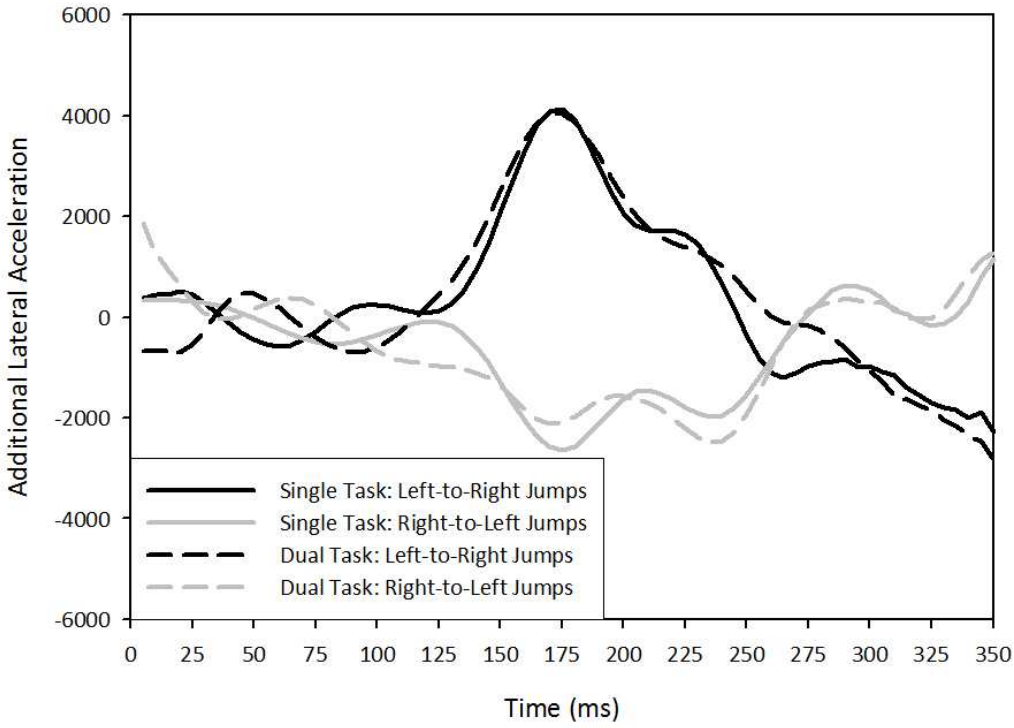
A 2 (task: single, dual) x 2 (perturbation: unperturbed, perturbed corrected) x 2 (target 1 location: left, right) repeated measures ANOVA was performed on the horizontal acceleration profiles.

There was no statistically reliable effect of task on the horizontal acceleration profile, so being under the dual task conditions did not affect the latency of the correction produced to the perturbation in the GO condition. As would be expected by the nature of the participant's task, there was more horizontal acceleration in the perturbed trials than the unperturbed trials beginning at 150ms [$p \leq 0.019$], as can be seen in Figure 13. There was also a significant effect of target 1 location, with more rightwards acceleration from the start of the movement up to 125ms, for targets initially presented on the right [$p \leq 0.042$], and then from 145ms, there was more rightwards acceleration for targets initially presented on the left and more leftwards acceleration for targets initially presented on the right [$p \leq 0.016$; see Figure 13]

In addition, there was also a significant perturbation x target 1 location interaction, with more lateral acceleration for rightwards jumping targets. This effect is observable in Figure 13, which plots the perturbed corrected acceleration values as a difference from the baseline performance. As can be

seen, there is greater lateral acceleration, with a sharper peak, for the left-to-right jumps (black lines). Figure 13 also clearly demonstrates the similarity of performance following the GO instruction under both single and dual task conditions.

Figure 13: The mean horizontal acceleration profiles for the perturbed trials in the Single and Dual tasks under the GO condition instruction. The perturbed trials are presented here as a difference from the unperturbed (baseline) trials. The perturbed trials with T1 presented on the left are plotted in black, and the perturbed trials with T1 presented on the right are plotted in grey. The single task performance is plotted in the solid lines and the dual task is plotted in the dashed lines.



Experiment 4: Discussion

The main aim of Experiment 4 was to investigate the preferential settings of the automatic pilot by observing the symmetry or asymmetry in the correction rates produced under cognitive load. Furthermore, Experiment 3 suggested that an increase in task difficulty could influence the correction rate and correction efficiency under single task conditions, and make the potential asymmetries

more clearly observable. By asking the participants to perform the manual aiming task under switching GO and NOGO task instructions, whilst concurrently attending to the n-back auditory task, it was hypothesised that under these respectively harder conditions, the automatic pilot's default or preferential setting would be revealed.

The task switching design of Experiment 4 appears to be effective in reducing the ceiling and floor rates of correction observed in Experiment 3. In the GO condition, single task performance reduced from 89% to 74% and dual task performance reduced from 92% to 77% when comparing the average individual correction rates between Experiments 3 and 4. The reverse pattern was also observable for the NOGO condition, with average individual correction rates increasing from 2% to 13% in the single task and from 3 % to 28% in the dual task, with the introduction of requirement to switch reach instructions. These findings clearly demonstrate the increased difficulty in following the task instructions when the attentional set keeps shifting, and confirms that prior experience can substantially modify the automatic pilot settings (Striemer et al., 2010).

Although there were costs for the rates of corrections produced in Experiment 4, in comparison with Experiment 3, the rates of correction produced on the current experiment did not differ for the GO instruction whether under single or dual task conditions. The rates of corrections did differ however, for the NOGO trials when under the single and dual task conditions. The NOGO performance during the single task was comparable to the NOGO performance in Experiments 1 and 2, yet this low rate of corrections significantly increased under the dual task conditions. This would suggest that the suppression of the automatic pilot, under the NOGO cognitive setting, is hard to maintain, and under heavy cognitive load begins to revert towards the default level. Thus, whilst voluntarily biasing the automatic pilot towards greater responsiveness

requires few or no cognitive resources, beyond the voluntary decision itself, disengagement of the automatic pilot would seem to take sustained effort.

This pattern of results replicates those in an anti-saccade task, which also used the n-back as a secondary task. The anti-saccade task (Hallet, 1978), much like the anti-point task (Day & Lyon, 2000; Johnson et al., 2002), requires cognitive resources to be performed, as a reflexive response, like a saccade, would need effort to be overridden or suppressed. Mitchell et al. (2005) also suggest that working memory may play a part in the anti-saccade task, as the participant may need to hold the instruction in memory, for example, 'look away from the target' and repeat it to themselves throughout the trials. Further evidence for the role of working memory comes from the fact that more errors occur in the anti-saccade task when performed under dual task conditions (Roberts, Hager, & Heron 1994; Mitchell et al., 2005), with the number of errors increasing with the difficulty of the dual task (Roberts et al., 1994).

Mitchell et al. (2005) found that when participants were asked to perform a pro- and anti-saccade task, along with a secondary n-back task, the error rate increased under the dual task conditions, with an increase in reflexive responding, with participants looking towards rather than away from the target. Further investigation in their second experiment revealed that the working memory load, induced by the n-back task, 'exerts quite specific effects on the control of saccadic eye movements' (Mitchell et al., 2005: p.100), with the extra cognitive load impairing the ability to suppress the reflexive response, but not disrupting the capacity to produce voluntary saccades. In reference to the current experiment, it appears that when following the NOGO task instruction and when concurrently performing the n-back task, the mental flexibility required to inhibit the need to correct is not available, and without this, the more reflexive or default behaviour is more likely to emerge.

Apart from the increase in corrections in the NOGO condition, the dual task did not impact on the other movement characteristics. There was an increased reaction time during the dual task blocks, in comparison to the single task blocks, but the secondary task did not affect the movement times, peak velocities or the times to reach peak velocity for the unperturbed or perturbed trials. Nor did the dual task conditions affect the spatial or temporal profile of the corrections, demonstrating that manual aiming movements are robust and can be executed efficiently under heavy cognitive load. As with all of the experiments in this chapter, Experiment 4 has demonstrated the bias in correcting towards the right, with significantly more corrections which are initiated earlier and are produced with generally faster movement times, higher peak velocities and quicker times to reach peak velocity.

In conclusion, Experiment 4 has shown that out of the GO and NOGO instructions, the GO instruction is more resilient than the NOGO and requires less effort to maintain. The GO response may be a more natural, environmentally valid, response, as one would expect it would be advantageous to be able to track a target and manually follow it to a new location. The NOGO response on the other hand, requires cognitive effort to inhibit the tendency to follow the target. This tendency is not so strong that it cannot be overridden when adequate cognitive resources are available, as demonstrated in the current and previously reported experiments; yet when under the dual task conditions, the rate of corrections does creep up as the resources needed to intentionally suppress the corrective response become less available.

General Discussion

The series of experiments reported in this chapter investigated the influence of cognition on the automatic pilot. Experiment 1 also introduced a new

instruction, which allowed an examination of the relationship between intention and the automatic pilot, and questioned the assumed automaticity of the automatic pilot. The automatic pilot was so named, as the corrections produced in the STOP condition of the Pisella et al. (2000) study, were uninstructed and appeared to occur 'automatically', without the participants' awareness. There is a misconception in the literature following Pisella et al.'s (2000) study, that the corrections produced in the STOP condition are *disallowed* and still occur, but there is a strong difference between being uninstructed (as in the STOP task) and being explicitly countermanded (as in the NOGO task). The results of Experiment 1 demonstrate the clear difference between the levels of corrections produced when they are uninstructed and when they are countermanded, and these results have since been replicated (Cameron et al., 2009; Striemer et al, 2010).

The rates of correction produced in the STOP condition in Experiment 1 are similar to other rates reported in similar experiments (Cressman et al., 2006), and a study using the NOGO condition, published after these experiments had been completed, also reports similar rates of correction when the participant is explicitly told not to correct towards the target in the new location (Cameron et al. 2009). The level of corrections reduces dramatically when the participant does not intend to correct, in comparison with the level of corrections produced when the participant is not instructed to correct. The NOGO Control Experiment (Experiment 2) confirms the use of the NOGO instruction as a valid instruction and verifies that participants performing the task under the NOGO instruction are able to complete the task in a similar way to participants performing in the GO and STOP conditions.

Although the participants are able to attend to the new target location and still accurately point to the original target location, it appears that this response set required cognitive resources to be maintained, and the NOGO task instruction may be the most difficult of the three experimental conditions to perform. The

rate of corrections in the STOP condition in Experiment 1, and the observation that performance in the STOP condition did not improve with practice suggests that the STOP condition may reflect the default level of corrections that the system produces without the influence of an instructed cognitive goal. The GO condition, appears to benefit from the cognitive desire to follow the target if it jumps, with a greater amplitude and higher rate of correction produced, compared to the STOP condition. The NOGO condition is also assisted by the cognitive goal set by the NOGO instruction. Participants are able to inhibit the need to correct towards the new target location, but this becomes increasingly difficult to maintain when cognitive resources become unavailable during dual task conditions.

The automatic pilot does like to track, and make corrections towards, a moving target, but this does not occur in a strong automatic sense. The automatic pilot is not strongly automatic, as the corrections can be overridden by conscious control, just as they can be boosted by an opposite cognitive setting or goal. However, the natural state of the online correction system does seem to be to follow the target to some extent, with the system reverting to the more reflexive corrective response when under heavy cognitive load. The level of corrections in the GO condition appears to be easily maintained, as they are not negatively affected when cognitive resources are running low, nor is either the GO or the NOGO performance affected by the switching instructions in the single task in Experiment 4. The findings from all of the experiments reported in this chapter suggest that the role of cognition appears central to the successful performance in the double-step task, with the attentional set, as determined by the task instructions, integral to the pointing behaviour produced.

The contribution of cognition to the performance in the double-step task qualifies the use of the term ‘automatic’ with reference to the automatic pilot for the hand. The ability to update movements online is susceptible to voluntary control, as demonstrated in Experiments 1, 2 and 4, and is sensitive to

concurrent cognitive load, as demonstrated in Experiments 3 and 4, contradicting the two features that need to be combined to identify a process as strongly automatic (Palmer & Jonides, 1988). The performance in the GO task however, does to some extent meet these criteria, with the level of corrections produced unimpaired by the dual task conditions, yet the level of corrections produced is likely to be a product of conscious intention. Performance in the GO condition has also been shown to be affected by the instruction to point sequentially to multiple targets, with less corrections towards a target perturbation if there is another target present (Cameron et al., 2007), providing an alternative method to address the load criterion for automaticity. The level of corrections produced in the STOP response condition may reveal the neutral state of the automatic pilot, which can be classed as weakly automatic, as corrections occur towards the new target location without being instructed and a concurrent cognitively demanding task does not negatively affect performance.

In addition to shedding light on the cognitive aspects of the automatic pilot, this series of experiments has highlighted two key characteristics of manual aiming movements: firstly, the individual variability in the ability to correct towards the target perturbation; and secondly the difference in the kinematics and correction rates of movements towards right and left presented targets.

In all four of the experiments described, the participants were all right-handed, performing the task with their right hands, and demonstrated an advantage for the online correction of movements towards right-sided or rightwards moving targets. Across the data, targets presented on, or jumping towards, the right result in faster reaction times, faster movement times, quicker correction times, higher peak velocities and a shorter time to reach peak velocity, along with being more accurate and producing more corrections towards the new target location, in comparison with movements and corrections towards targets presented on the left side of the screen. Day & Lyon (2000) also found more

deviation towards right targets in participants using their right hands. One factor to bear in mind is that there is only a small five degree difference between the left and the right target presentation locations for such a difference in these movement characteristics to be evident. If this rightwards skew is due to the right-handedness of the participants and there is a biomechanical or hemispheric compatibility explanation (e.g. Fisk & Goodale, 1985), then it would be expected that left-handed participants would demonstrate a leftwards advantage. However, if it is more the case that rightward corrections are controlled by the left hemisphere, which may be specialised for reaching and grasping (Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007), then it would be expected that rightward target jumps would be preferentially processed independent of handedness. This question is addressed later in this thesis, in Experiment 9.

Chapter Three:

Attentional aspects of the automatic pilot

Chapter Three addresses the attentional aspects of the automatic pilot system. The intention of this series of four experiments is to establish what visual factors of the double-step paradigm are driving the automatic pilot, and which aspects of the target stimulus and the target perturbation 'capture' the attention of the visuomotor system. Furthermore, to gain understanding of whether the incoming visual information that is selected-for-action, as indicated by the automatic pilot response, has characteristics similar to the visual information known to be selected-for-perception. As discussed in previous chapters, the double-step task allows the investigation of how the motor system detects, and corrects for, motor errors. This can be investigated by manipulating the visual factors of the target stimulus, including the characteristics of the jump. The main task within the double-step paradigm is for the motor system to detect an error or mismatch between the intended target of the movement and its current predicted endpoint, and implement the correction, thus providing a context to understand visual attention under specific task conditions.

The double-step task involves the simultaneous offset of a target and the onset of a similar target at a new location. This sequence of events is perceived, through the phenomena of beta motion (Wertheimer, 1961), as a coherent 'jump' and participants perceive the new target as the original target they were tracking (Kahneman et al., 1992; Mittroff et al., 2004). The visual attention literature indicates that onsets receive priority processing over offsets (Cole, Kentridge, Gellatly, & Heywood, 2003) and over other visual elements, such as

luminance, colour, and shape. Although unique salient stimuli can be used to drive an efficient visual search, they are not sufficient to pull attention to their location (Jonides & Yantis, 1988). Abrupt onsets appear to be the most efficient stimuli for capturing attention in a bottom-up manner.

Although this attentional allocation has been established as efficient, it has not been confirmed whether the features of the attentional capture meet the two criteria for automaticity, discussed in Chapter 2. In previous studies, it has been confirmed that the presence of an increasing number of distractor letters in a visual search display does not affect the time taken to identify the target when that target was abruptly onset (Yantis & Jonides, 1984; Jonides & Yantis, 1988; Franconeri & Simons, 2005). The fact that there was no increase in reaction time with the increase in set size was taken to suggest that onsets were 'processed first regardless of their identity and position' (Yantis & Jonides, 1990. pg. 122) and therefore the priority allocation of attention to an abrupt onset was thought to be an automatic process, as the concurrent load criterion had been met. For the capture of attention by an abrupt onset to be classed as strongly automatic, then the abrupt onset would have to have priority over all other stimuli in the visual field, regardless of any voluntary allocation of attention in response to any pre-cue information (Yantis & Jonides, 1990).

In a test of the intentionality criterion, Yantis and Jonides (1990) used a set up in which one original placeholder and one dotted placeholder (which was made up of six dots, one at each location where the lines in the original placeholder would have met) were displayed either side of a fixation cross, which were then replaced by one target letter and one distractor letter on each trial. There was an 80% valid cue arrow indicating the side of the display in which the target would appear, and the target would either be abruptly onset or revealed using the no-onset procedure. Yantis and Jonides (1990) found that the abrupt onset was not able to account for the reaction time differences to identify the target under the different manipulations. The pre-cue validity determined the

allocation of attention, although this interacted with the type of target presentation. When participants were already attending to the location indicated by the pre-cue, an abrupt onset did not result in quicker identification over a no-onset presentation, however when the participant was miscued, the participant was faster to respond to a target with an abrupt onset than a no-onset presentation. Further analysis confirmed that the effect of target presentation was larger when the cue was invalid, which suggests that onsets do not receive priority processing irrespective of the rest of the visual scene. An automatic capture of attention would have ensured the onset target was processed first regardless of the current locus of attention when the target was onset. The fact that when attention was initially miscued, onsets were identified more slowly than when presented after a valid cue implies that the intentionality criterion was not fully met (Yantis & Jonides, 1990).

A further manipulation of stimulus onset asynchrony (SOA) confirms that prior allocation of attention can prevent the capture of attention by abrupt onsets. When a 100% reliable cue arrow was presented 200ms before, simultaneous to, or 200ms after the presentation of the letters, attentional prioritisation of the abrupt onset was cancelled by the voluntary pre-allocation of attention to the known location of the to-be-presented target letter. The reaction times to the target letter, whether it was presented as an onset or a no-onset, were virtually identical. Importantly, when the target was a no-onset presentation, there would have been an abrupt onset somewhere else in the stimulus display, which did not distract from the no-onset target identification. The valid cue presented 200ms beforehand prevented the non-relevant onset from capturing attention. In the other two conditions, 0ms and +200ms SOA, the cue arrow was not of much use to the participant in identifying the location of the target. In these conditions, there was a significant difference in the reaction times to targets depending on the method of presentation, with targets with an abrupt onset being identified much faster than when one of the distractor letters was abruptly onset (Yantis & Jonides, 1990). The third experiment in the Yantis and

Jonides (1990) study provides further support for their finding that when attention is already allocated to a location, an abrupt onset elsewhere in the visual field will not capture attention (Yantis & Jonides, 1984).

These findings have been replicated by Theeuwes (1991), who also set out to test the intentionality criterion for onsets and offsets. Using a similar paradigm to Yantis and Jonides (1984; Jonides & Yantis, 1988), Theeuwes had participants search for a target letter amongst three non-target letters. The letters were presented using the no-onset procedure and a 100% reliable central cuing arrow was gradually onset, at three different SOAs. Instead of one of the letter stimuli being onset, as in the Yantis and Jonides (1984) paradigm, a line segment was abruptly onset near to one of the letters. In the Theeuwes (1991) paradigm it would be advantageous to ignore the onset, as the cue arrow pointed to the correct location on all trials. However, when the central cue was presented late (+200ms SOA), reaction times to the target with the near onset were faster than the reaction times to targets when the onset was at a non-target location. The onset captures attention and holds it, so that when the central cue is presented, attention has already been captured, even when there is no benefit to paying attention to the onset transient. At the -600ms SOA, the effect is reduced, as the cue is presented before the display is revealed and the onset has occurred. In this condition, attention has already been voluntarily focused at the location directed by the cue arrow and the onset, in an unattended location, does not capture attention. The search starts at the location of the onset and then moves onto the other stimuli. If the target is the letter near to the onset, reaction times are fast, but if the onset is near a non-target location, it takes time for attention to be disengaged and to move round to find the target, making responses slower (Theeuwes, 1991). In the other conditions, when attention is focused towards the target location, there is no effect of the onset on reaction times.

Theeuwes' (1991) data and the findings from Yantis and Jonides (1990) illustrate that the capture of attention by abrupt onsets does not fulfil the intentionality criterion for automaticity. 'The extent to which abrupt onsets capture attention is under the control of the subject's intentions rather than under the control of stimulation' (Theeuwes, 1991. pp. 87). Thus, although onsets can capture attention and the reaction time to identify an onset is independent of the display size, the capture of attention by onsets cannot be classed as strongly automatic (Yantis & Jonides 1984; Jonides & Yantis, 1988). The visual attention system does give priority to onsets when attention is diffused across the visual scene, but does not allow onsets to distract attention when attention is pre-engaged and highly focused on a specific location. The capacity for an abrupt onset to capture our attention therefore may depend on the participant's attentional set and the specific demands of the task.

And so it seems that within a real world setting, the attentional set and the goal demands drive the allocation of attention. Unique colour, luminance, onsets and motion can appear to be very salient, but the attentional system has the power to resist all of these visual features if they are unrelated to the task in hand. The experiments reported in Chapter 2 support the idea that goal demands will determine whether or not the target jump 'captures' the hand's trajectory. In the NOGO task, when participants were required to ignore the target jump, *and the likely jump location was completely predictable*, participants were able to suppress online corrections almost entirely (see also Cameron et al, 2009; Striemer et al, 2010).

This is consistent with the idea that the attentional processes of selection-for-action operate similarly to, or even be identical with, those of selection-for-perception. However, this need not necessarily be the case. Indeed, given the well-established neuroanatomical and functional division between vision-for-perception and vision-for-action, it is possible that distinct attentional mechanisms could subserve these two classes of behaviour, and that these

attentional mechanisms could have different characteristics (e.g. Milner, 1995; Milner & Goodale, 1995). The automatic pilot is located within the dorsal stream (Desmurget et al, 1999; Pisella et al, 2000), which is specialised for quick analysis of spatial information to guide action, whereas the ventral stream is responsible for visual object recognition, and is slower to process this information (Goodale & Milner, 1992; Desmurget et al, 1999). The functional specialisation may be reflected in different attributes being more significant for attentional capture in perceptual and action-based contexts. As will be discussed later, not all visual information can be used to drive fast hand movements (Veerman et al., 2008).

The visual attention literature demonstrates that the attentional set is important and that the task requirements help the system to filter the incoming information and perform the task effectively. In a visual search task, the visuoperceptual system will not be drawn to an irrelevant object if that object's features are not part of the attentional set appropriate for target identification. However, if the requirement is to identify a target that is defined by one single feature, then any other objects that are also defined by a single but different feature may also have the potential to capture attention. It appears in this situation that the attentional set is not so rigid, but in other circumstances can be so strictly set that participants do not perceive a gorilla walking through the visual scene (Simons & Chabris, 1999).

Visual attention paradigms can alter the attentional set and the task instructions, so that different features within the same scene become the targets and the distractors. Also, the attentional set can also be monitored at a 'default' setting, or with the task demands removed altogether, by telling participants to view a scene and memorise it for a later memory test or to provide an aesthetic judgement (Pasher & Harris, 2001). Performing these manipulations reveals that there is a strong tendency to remember or attend to the unique item in the visual scene, although Pasher and Harris (2001) warn that 'attention shifts to

transients and to unique items should not be described as *involuntary*, it seems, but rather as *contingently involuntary* (i.e., the tendency can be voluntarily "turned off" or suppressed when it is not necessary for performing a given task)' (Pasher & Harris, 2001, pg.751).

The studies in Chapter 2 have demonstrated that automatic manual corrections towards a target perturbation can also be 'turned off' or suppressed in line with the goal of the task in the NOGO condition. As with the findings from the visual attention literature, one would expect that the visual information selected for action would be drawn to aspects of the environment exogenously but that the goal and task requirements would determine the extent of the attentional capture. One difference between the visual paradigms, and the double-step task used in this series of experiments, is that the double-step task relies on information selected-for-action. The features of the stimuli that are selected for action have to depend on visuomotor system settings and these may or may not be similar to those employed by the visuoperceptual system.

Being a dorsal stream function, it would be expected that attributes such as movement and luminance would capture attention over features such as colour and form. Three studies all using a double-step task investigated the ability to use colour information to drive fast manual corrections. The double-step task involves the simultaneous offset of a target and the onset of a similar target at a new location. This sequence of events is perceived, through the phenomena of beta motion (Wertheimer, 1961), as a coherent 'jump' and participants perceive the new target as the original target they were tracking (Kahneman et al., 1992; Mittroff et al., 2004). Pisella et al. (2000) employed a colour-go and a colour-stop condition, in which a red and a green target were presented, with the participant's task being to touch the green target. On a proportion of the trials, the red and green target would swap places upon movement commencement, and so in the colour-go task, participants had to touch the green target in the new location, and in the colour-stop condition, they had to abort their

movement in reaction to the colour perturbation. Pisella et al. (2000) found that there were no corrections made towards the new target location before the movement was aborted in the colour-stop condition and that the corrections that were made in the colour-go condition involved a significant increase in movement time. This result was interpreted by the authors as suggesting that the automatic pilot was specific to location processing, perhaps consistent with a dorsal stream localisation.

A kinematic analysis of performance using a similar paradigm revealed that in aiming movements towards a colour perturbation in the colour-go condition, there was a reduced rate of corrections, with the corrections being produced later in the trajectory and resulting in a longer movement time, in comparison with performance in the location-go condition (Cressman et al., 2006). In addition, Cressman et al. (2006) also reported a high rate of not-stops in the colour-stop condition, with participants failing to interrupt their ongoing movement in response to the colour change. The delay in being able to respond to a colour change is presumed to be due to the differences between channels in the brain that process incoming visual information. In very simplified terms, a distinction is made between object properties, such as location and colour, as early as in the retina. The M ganglion and the P ganglion cells in the retina project to the magnocellular and parvocellular cells in the lateral geniculate nucleus, which then go on to terminate in different regions of V1 (Livingstone & Hubel, 1987) and then on to the structures that make up the two cortical visual streams. The magnocellular cells are large cell bodies that can carry information about location quickly, but without much detail. In comparison, the parvocellular cells are small and carry information in lots of detail, such as colour, but the ventral stream takes longer to transport and process these details. As a result of comparing manual aiming movements towards stimuli that were designed to be detected exclusively either by the parvocellular or the magnocellular channels, Brenner and Smeets (2003) concluded that “fast responses appear to be colour-blind” (pg. 249). The two types of stimuli used

were discriminated using low and high temporal resolutions. The parvocellular stimulus was an isoluminant red and green checkerboard, which was indistinguishable from the surrounding background on all attributes other than chromaticity. The magnocellular stimulus was a square defined by a 30 Hz luminance flicker, which alternated between a black and a yellow square, and again, was indistinguishable from the yellow background, as chromaticity and luminance had been controlled for. It took 35ms longer to respond to a target location perturbation that could only be detected by the parvocellular pathway, in contrast to a flickering target location change, leading Brenner and Smeets (2003) to conclude that the parvocellular channels that process the chromatic information are not fast enough to trigger fast online corrections, due to the properties of the neurones involved and their less direct connection to the visuomotor areas of the dorsal stream.

Nevertheless, the following year, Brenner and Smeets (2004) published a paper called 'Colour vision can contribute to fast corrections of arm movements', which claimed that corrections towards a colour perturbation, in which a red target and a green distractor swap places, can be detected in the movement trajectory as little as 120ms after the target has moved. The authors reconcile their contrary results to Pisella et al.'s (2000) findings by suggesting that the colour-stop condition required participants to have to change the task and initiate a new movement, and that it is the new movement that takes additional time. The results from Cressman et al. (2006) address this issue by including a colour-go condition, with participants instructed to touch the green dot, and demonstrated the altered trajectories descried above. The longer movement times and later corrections demonstrated by Cressman et al. (2006) are evident in the Brenner and Smeets (2004) study, with longer latencies (up to 50ms) to correct towards the red target when there was a green square also present. Although the title of their paper suggests that there is a contribution of chromatic information, the authors concede that 'fast on-line corrections do not always occur automatically' (Brenner & Smeets, 2004, p. 306) when the target

at a new location has to be distinguished from a distractor on the basis of colour. It takes time for the colour information to be processed, by which time voluntary attentional resources can be utilised, and conscious corrections can be directed towards the target identified by colour.

The 50ms additional latency for corrections to targets identified by colour has been replicated by Veerman, Brenner and Smeets (2008), in a comprehensive study which systematically varied the visual attributes of targets in manual reaching using a single methodological paradigm. In order to establish which target attributes were successful at capturing attention and driving manual corrections, Veerman et al. (2008) varied the attributes that distinguished the target from two reference objects over a series of blocked conditions. In each condition the target differed from the two reference objects in grades of luminance, orientation, size, colour, shape or texture. These conditions were compared to a control condition, in which the reference objects were the same colour as the background, and so were invisible to the participant and only the dark grey target could be seen. The participants were instructed to reach for the target and to adjust their hand movement to reach the new target location if the target changed position, which occurred on 50% of trials.

Veerman et al. (2008) were interested in the responses to changes in target position as indexed by the latencies and intensities of the corrective responses. The latency of the response to the change in target location was estimated by determining the amplitude of the peak in the additional lateral velocity of the initial response (calculated by the difference between the lateral component of the perturbed and unperturbed trials), fitting a straight line through the points at which the additional lateral velocity reached 25% and 75% of this peak value, and identifying the time of intersection of this fitted line with the line of additional lateral velocity of zero. The magnitude, or intensity, of the correction was estimated by averaging the peak lateral velocities in the perturbed trials for

each condition to determine whether any systematic differences between the intensity of the different participant's responses could be identified.

Participants were slower to correct in the perturbed trials towards the targets identified by shape, colour and texture, with responses 50ms longer than those to targets identified by luminance, size and orientation (Veerman et al., 2008). This distinction between these visual attributes fits well with the dorsal/ventral distinction (Goodale & Milner, 1992; Desmurget et al., 1999), supporting the idea that the attributes required for object recognition (shape, colour and texture) are processed by the ventral stream and do not support rapid online correction, a dorsal stream specialisation (Desmurget et al., 1999). Veerman et al. (2008) also carried out an extensive exploration of the effect of the conspicuousness of the target in comparison to the distractors using seven different luminance conditions. The authors were able to conclude that the perturbation of a less conspicuous target resulted in a less vigorous response with regard to the horizontal acceleration of the hand, and also in more variability in the latency of the response. Using these data, Veerman et al. (2008) were able to check that the 50ms delay in initiating the correction towards the target when it was defined by colour, shape or texture, was not due to a reduced conspicuousness of the target, as the magnitude of the response did not differ.

The intensity of the correction did not differ between any of the conditions. When Veerman et al. (2008) aligned the mean lateral velocity profile for each of the conditions, irrespective of the timing, there was a similar pattern of response, suggesting that the intensity of the correction did not differ, but the latency of the initiation of the correction did. Although performance between the conditions did not differ in the intensity of the correction, Veerman et al. (2008) reported individual variability between the participants in their intensity of responses. Participants whose corrections were less intense in one condition, tended also to perform with a lower intensity in all conditions. This

does not, however, imply that participants were just producing a pre-programmed response to all perturbations, as the characteristics of the response were systematically related to the visual change. For instance, the strength of the correction in the 6cm jump conditions was twice that of the 3cm jump conditions (Veerman et al., 2008).

In the studies described above (Pisella et al., 2000; Cressman et al., 2006; Brenner & Smeets, 2003; Brenner & Smeets, 2004; Veerman et al., 2008), the methodologies require reference or distractor stimuli to be presented in addition to the target stimuli, in order to ensure that target identification is due to the manipulated stimulus attribute. This method is employed in Experiment 5 to allow the manipulation of the salience of the target jump. The rationale behind Experiment 5 was to determine the role of stimulus salience (luminance) in modulating autopilot efficiency. This was considered as a sensible starting point, as the visual attention literature identifies salience as an important attribute modulating the capture of attention. If the visual and the motor systems respond to similar properties, then presumably, target salience will attract the attention of the motor system, with a more salient jump leading to more automatic pilot driven corrections. Given the conceptual similarity of this series of Experiments to the studies on the effects of target luminance reported by Veerman et al. (2008), it must be emphasised that all of the experiments reported in this chapter were completed before the publication of Veerman et al.'s paper.

Experiment 5: Methods

Participants

Nine naïve adult volunteers (5 females and 4 males, mean age: 18.5 years, SD: 1.13) took part in the study. All the volunteers were recruited amongst the Undergraduates in the Psychology Department at the University of Edinburgh and received course credits for participating. All of the participants were right-handed and reported no visual or motor deficits.

Design

The study was made up of three within-participants conditions, a High salience condition, a Mid salience condition and a Low salience condition. Each condition consisted of 60 trials, with a 30% perturbation rate. There were two stimulus presentation locations, 35mm to the left and 35mm to the right of the centre of the screen. In the unperturbed trials, the target dot was always presented on the left side and in the perturbed trials, the target dot always jumped from left-to-right.

The stimuli were presented in two blocks of 180 trials each, one block under a GO instruction and the other with a STOP instruction. Block order was counterbalanced across participants. The participant was given 20 practice trials before the start of each block. All stimuli were presented in a random order and a break was given to the participant between blocks. At the end of the second block, eight calibration trials were recorded, with the index finger positioned on the response button, the centre of the screen and 35mm to the left and to the right of the centre (two recordings made at each location), to provide reference points for the calculation of spatial errors.

Apparatus and stimuli

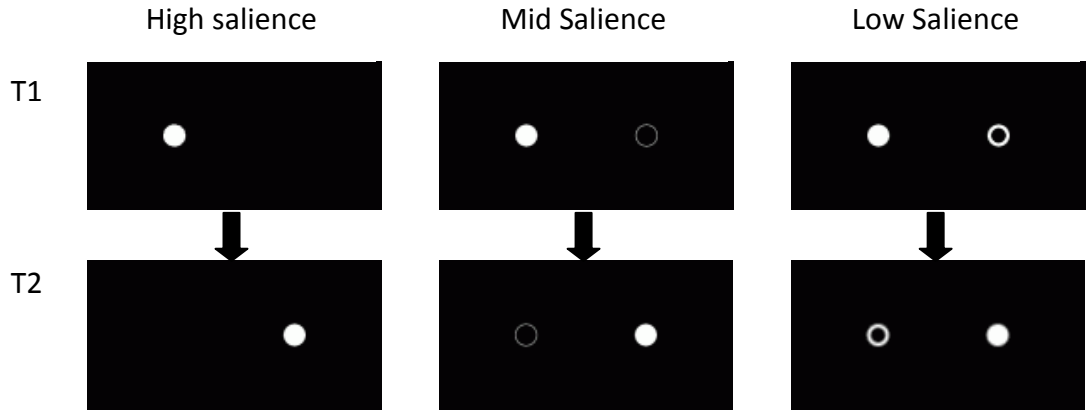
The participant sat or stood (depending on height) at a projection table with their chin in a chinrest (415mm from presentation surface) and their right-hand index finger resting on the start button. Stimuli were presented on a projector table (active display area 1000 x 750 mm, resolution 1024 x 768 pixels), approximately 480 mm from the response button, in a dimly illuminated room. The target stimulus was a white dot, 13mm in diameter, presented on a black background to reduce glare. On all trials, the stimuli appeared 35mm to the left of the centre of the screen when the button was pressed, and either stayed in its initial position (unperturbed trials) or made a jump to 35 mm to the right of the central position in the perturbation trials, upon button release.

As demonstrated in Figure 14, in the High salience condition, the unperturbed trials involved one filled white circle presented on the left of the midline and in the perturbation trials, the filled white dot jumped to the right of the midline.

In the Mid salience condition, the unperturbed trials involved one filled white circle presented on the left of the midline and a one-pixel white outline of a circle presented 35mm to the right of the midline. In the perturbed trials, the filled white dot jumped to the right of the midline, and so the filled dot and the outline swapped places.

In the Low salience condition, the unperturbed trials involved one filled white circle presented on the left of the midline and a five-pixel white outline of a circle presented 35mm to the right of the midline. In the perturbed trials, the filled white dot jumped to the right of the midline, and so the filled dot and the outline swapped places.

Figure 14: Example stimuli of perturbed trials from Experiment 5 (not drawn to scale). The target is the white filled dot and is always presented on the left location on the screen, jumping to the right location in the perturbed trials. In the unperturbed trials, the T1 stimulus is presented in both the T1 and T2 presentations, and so the target does not move. There are unperturbed trials for each of the three conditions.



Infrared tracking equipment (Optotrak: Northern Digital Inc., Waterloo, Ontario, Canada) was used to record the kinematic features of the aiming movement from commencement to cessation at 200Hz for the duration of 1 second. One infrared diode was secured to the participants' right index finger.

Two tones were used to pace the participant's movements, as described in Experiment 1.

Procedure

The procedure and GO and STOP task instructions were as described for Experiment 1, with the additional emphasis that the target was always the filled white dot.

Experiment 5: Results

Unperturbed Trials

Table 12 contains the mean data for each of the dependant variables in the unperturbed trials in Experiment 5.

Condition	Task	RT	MT	PV	TPV	AE
High Salience	GO	425.00 (181.02)	409.44 (27.86)	2126.71 (148.37)	134.44 (22.60)	1.09 (0.36)
	STOP	448.22 (175.27)	433.06 (28.33)	1981.14 (193.28)	143.61 (26.46)	1.00 (0.41)
Mid Salience	GO	449.83 (223.35)	413.89 (33.98)	2124.53 (177.73)	136.67 (21.40)	1.00 (0.37)
	STOP	445.11 (172.63)	429.17 (25.98)	1970.38 (174.79)	142.78 (27.77)	1.04 (0.35)
Low Salience	GO	438.06 (207.34)	421.94 (29.28)	2107.42 (143.77)	133.06 (25.85)	1.05 (0.48)
	STOP	439.72 (163.30)	437.22 (23.86)	1975.20 (175.58)	145.83 (27.27)	1.00 (0.35)

Table 12: Means for the unperturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets) in the High, Mid and Low Salience conditions.

A repeated measures analysis of variance (ANOVA) was performed separately on RT, MT, PV, TPV and AE with task (GO, STOP) and condition (High salience, Mid salience, Low salience) as within subjects factors.

There was a main effect of task for PV [$F(1,8) = 13.93$; $p<0.05$], with participants reaching higher PV under the GO task instructions, which is supported by a trend in MT [$F(1,8) = 5.25$; $p=0.051$], with people tending to move quicker in the GO task. There was no effect of task on the other dependent variables [RT, TPV, AE: $p\leq0.175$]. MT was the only variable affected by the salience condition [$F(2,16) = 3.941$; $p<0.05$], with longer MTs in the Low salience condition, for both the GO and the STOP task instructions. The Low salience condition involved the most salient irrelevant item concurrently presented on the screen,

and thus presents a confound between the salience of the target and the salience of the placeholder. None of the other dependent variables were affected by the salience condition in the unperturbed trials [RT, PV, TPV, AE: $p \leq 0.488$].

Perturbed Trails

Table 13 shows the percentage of perturbed trials that were in a corrected position in the final frame of the movement. As can be seen, there is a high incidence of corrected trials under the GO task instruction in all three of the salience conditions, and in the STOP task, about 50% of all perturbed trials were in a corrected position before the hand was pulled back. Thus, only the corrected perturbed trials will be included in further analysis. Additionally, due to the differences in the task instructions and in the required behaviour for each, the following analysis of corrected trials is conducted separately for the GO and STOP tasks.

Condition	Task	RT	MT	PV	TPV	AE	Percent Corrected
High Salience	GO	450.61 (206.07)	381.67 (24.11)	2167.35 (153.22)	131.39 (24.18)	0.65 (0.46)	93.9%
	STOP	431.19 (189.86)	379.06 (44.00)	2021.45 (219.42)	145.31 (25.93)	-2.94 (1.64)	53.9%
Mid Salience	GO	434.39 (184.23)	398.61 (23.32)	2124.70 (155.13)	134.72 (21.92)	0.15 (1.23)	92.2%
	STOP	439.67 (177.03)	394.44 (47.32)	1985.48 (160.90)	141.11 (21.87)	-3.28 (1.58)	52.8%
Low Salience	GO	432.11 (199.50)	402.22 (28.27)	2149.80 (168.03)	136.94 (22.25)	0.14 (0.63)	93.9%
	STOP	449.33 (220.40)	398.33 (40.47)	1914.04 (232.11)	142.22 (40.65)	-4.07 (1.15)	50.0%

Table 13: Means for the perturbed corrected trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets) in the High, Mid and Low Salience conditions.

Go Task

A 3 (condition: High salience, Mid salience, Low salience) x 2 (perturbation: unperturbed, perturbed corrected) repeated-measures ANOVA was performed separately on MT, PV, TPV and AE.

For MT there was a main effect of condition [$F(2,16) = 21.494$; $p<0.001$], with participants moving quicker in the High Salience condition, and a main effect of perturbation [$F(1,8) = 10.223$; $p<0.05$], with faster movement times in the perturbed trials in comparison with the unperturbed trials. Neither the stimulus condition nor the perturbation had an effect on the peak velocity reached or the time taken to reach peak velocity [condition: $p\geq0.281$; perturbation: $p\geq0.249$].

The main effect of condition on AE narrowly failed to reach significance [$F(2,16) = 3.396$; $p=0.059$], suggesting a trend for smaller errors in the Mid and Low salience conditions compared to the High salience condition. Figure 15 indicates that in the trials where there was placeholder in the to-be-jumped-to position, participants were more accurate in their finger position at the end of the movement. There was also a main effect of perturbation for AE [$F(1,8) = 8.387$; $p<0.05$], with larger errors in the unperturbed trials compared to the perturbed trials. Figure 15 also demonstrates that the end-point errors in the unperturbed trials were all rightwards, even though the target was always presented in the left presentation position. This is likely to be due to there being only one perturbation direction and may reflect a preparedness to correct towards the new rightwards target location. Furthermore, the corrections towards the target in the High Salience condition were hypermetric, and overshot the target location.

Figure 15: Directional AE with respect to final target position, plotted in degrees for the unperturbed (black bars) and the perturbed corrected (grey bars) trials in the GO task

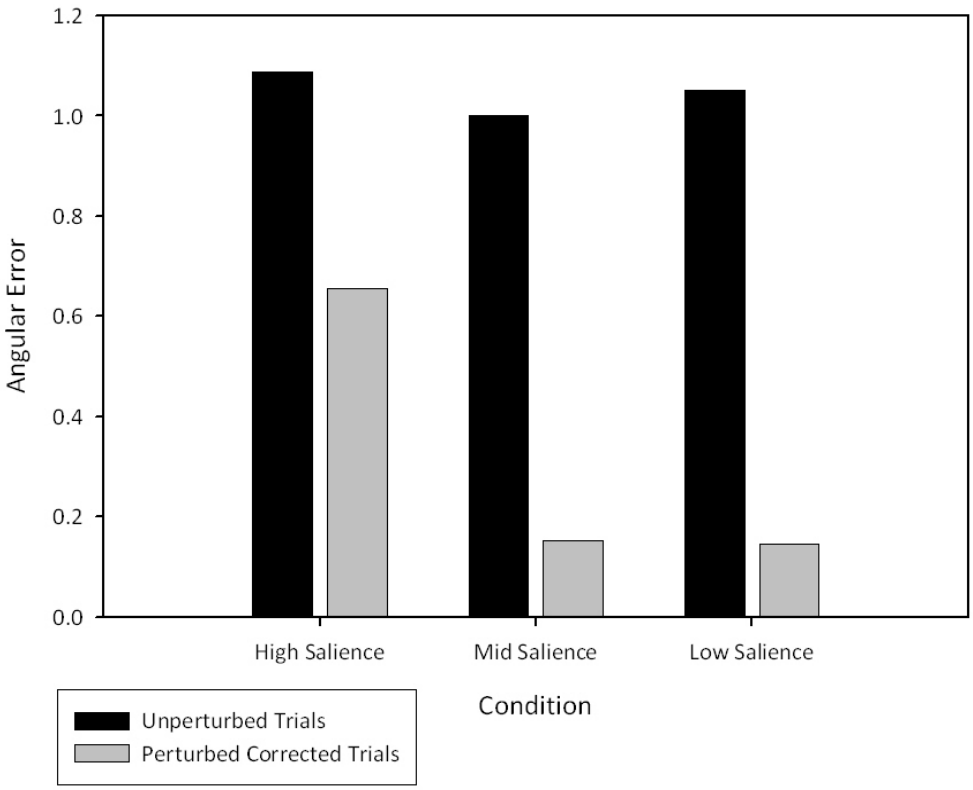
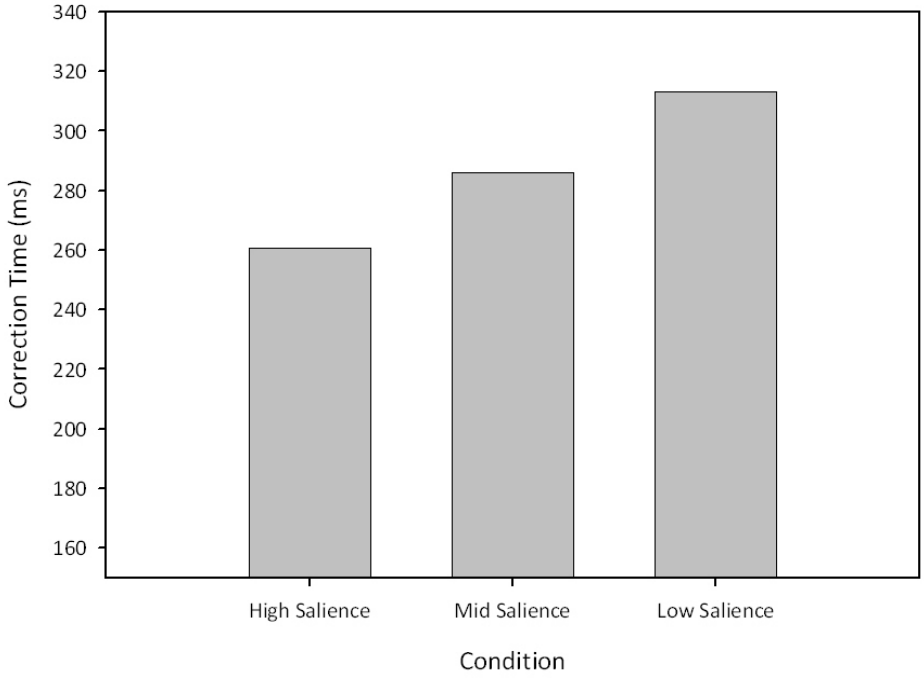


Figure 16: The Correction Time plotted in milliseconds for the perturbed corrected trials in the GO task



The correction time analysis, performed using perturbed corrected trials, revealed a main effect of condition [$F(2,16) = 20.89$; $p<0.001$]. Planned contrasts revealed that in the High salience trials, participants corrected their movements faster than in the Mid salience trials [$F(1,8) = 11.55$; $p<0.01$] and that in the Mid salience trials, participants corrected their movements faster than in the low salience condition [$F(1,8) = 9.64$; $p<0.05$], as demonstrated in Figure 16.

Stop Task

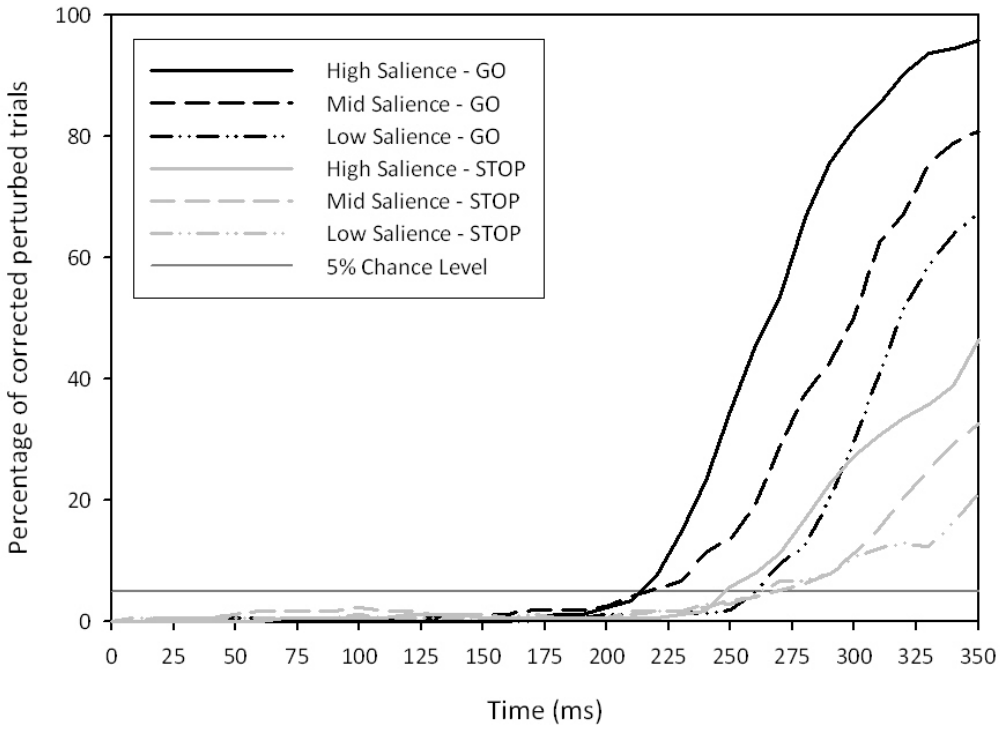
Table 3 reports the mean values for correction time and stop time and the percentage of corrected perturbed trials that were successfully stopped during the trial. Separate analyses of correction time by condition [$F(2,10) = 0.751$; $p=0.497$], Stop time by condition [$F(2,14) = 2.155$; $p=0.153$] and Stop rate by condition [$F(1.169,8.181) = 0.292$; $p=0.639$], revealed no significant difference between the three conditions. Although the means in Table 14 for correction time suggest a clear trend of shorter correction times with increasing saliency, there was not enough power for the effect to be significant, as four of the nine participants corrected on less than five perturbed trials in the STOP task.

	High Salience	Mid Salience	Low Salience
Correction time	278.9 (74.5)	311.4 (49.8)	330.9 (62.5)
Stop time	380.4 (45.8)	393.1 (46.7)	395.9 (39.6)
Stop rate	84.9%	89.5%	90.6%

Table 14: Mean correction time and mean stop time in corrected and stopped perturbed trials (ms) and percentage stop rate in corrected perturbed trials. (Standard deviations given in brackets).

Individual Corrections

Figure 17: The mean rates of individual current corrections for the three salience conditions, High, Mid and Low, in the GO and STOP tasks.



A mixed-model ANOVA was performed on the rate of individual corrections for each 10ms of the movement up to 350ms (35 levels), with task (GO, STOP) and condition (High salience, Mid salience, Low salience) as within subjects factors.

In order for any effect to be considered, it had to remain significant for 50ms (10 consecutive temporal bins). At 220ms, the effect of task becomes reliable [$p \leq 0.041$], with the GO task instructions resulting in significantly more corrections than the STOP task instruction (see Figure 17). From 230ms there is a main effect of condition [$p \leq 0.05$], with more corrections for the most salient target jumps in the High Salience condition, followed by the Mid Salience condition and the Low salience condition. There is also a reliable task x condition interaction from 230ms [$p \leq 0.017$], with the differences between the salience conditions taking longer to emerge clearly in the STOP task.

Horizontal Acceleration Profiles

Go Task

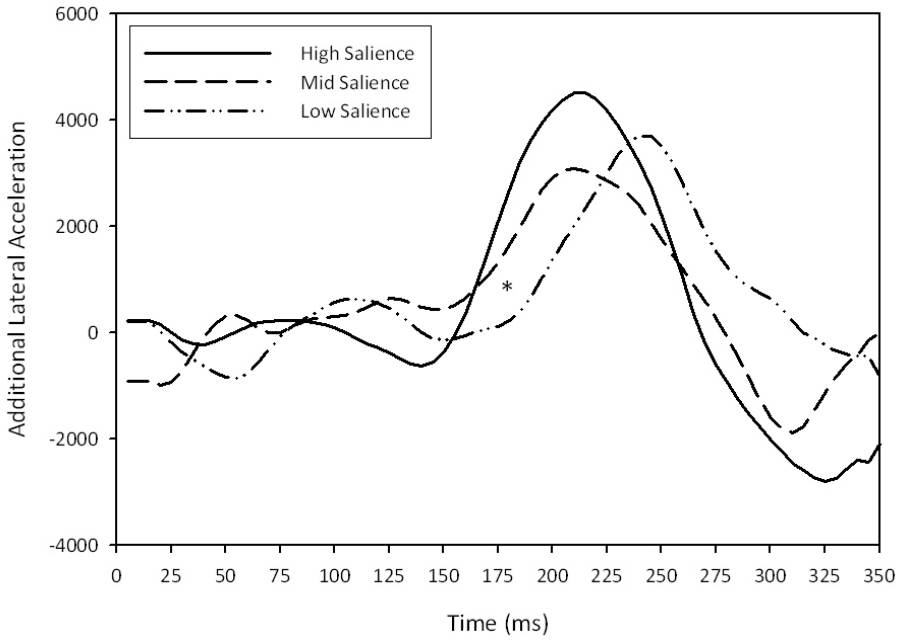
A paired-samples t-test comparing the unperturbed and the perturbed trials for each condition separately revealed that corrections in the High salience condition occur at 175ms, whereas the corrections in the Mid and Low salience conditions occur at 235ms and 240ms respectively. The salience of the target jump affects the latency of corrections made under a Go task instruction.

A repeated-measures ANOVA on additional horizontal acceleration was performed separately for the two tasks, GO and STOP, on condition as a difference from baseline (High salience, Mid salience, Low salience). In order for any effect to be considered, any effect had to remain significant for 50ms (10 consecutive temporal bins). The effect of condition becomes statistically reliable at 180ms [$p \leq 0.049$], with the High salience condition producing significantly more rightward acceleration than the Low salience condition.

Stop Task

A repeated-measures ANOVA on additional horizontal acceleration was performed separately for the two tasks, GO and STOP, on condition as a difference from baseline (High salience, Mid salience, Low salience). There were no statistically reliable effects in the STOP task for any of the conditions.

Figure 18: The additional lateral acceleration for the perturbed corrected trials, as a difference from baseline performance in the GO task. * denotes the time at which the High and Low salience conditions become significantly different from one another



Summary

Unsurprisingly, the salience of the target perturbation reliably affects the corrective movements made towards the new target locations. In the GO task for the High salience stimuli, there were the highest rates of corrections and the earliest initiated corrections, in comparison with the Mid and Low salience conditions, as revealed by the correction time and lateral acceleration analyses. Although the High salience stimuli resulted in shorter movement times and shorter correction times, the end points of the movements in these trials were less accurate suggesting a difference between the spatial and temporal aspects of the movement. The rightwards error may well be due to the increased rightward vigour towards the direction of the target jump, resulting in hypermetric corrections. When there is a full simultaneous offset and onset, as in the High salience condition, participants are faster to move to the new target location but overshoot the new target location, whereas in the Low salience condition, where there is a five pixel outline of a circle indicating the new

location, movements were slower but more accurate. This may be more than just a speed-accuracy trade off, because in the analysis of the unperturbed trials, the thick outline slowed down the movements even when the target did not move. It may be that having the outline in the to-be-jumped-to-location allows the system to plan an alternative movement to that location in advance (in case the target is perturbed), but it takes longer to initiate this alternative plan because the imperative change is less salient.

Experiment 5: Discussion

In the visual attention literature, luminance change was found by Yantis and Hillstrom (1994) to be neither necessary nor sufficient for capturing attention in a bottom up manner. This appears to go against the findings from the current study and those of Veerman et al. (2008), which both suggest that luminance is capable of capturing attention and driving manual corrections. In the Veerman et al. (2008) study, after the control condition, the 390% luminance difference condition produced the greatest lateral acceleration, of all the other experimental conditions, and in the current study the high salience and most-luminant condition resulted in the earliest and most vigorous corrections. Thus, our findings replicate the results of the Veerman et al. (2008) study. The difference between the conclusion within the visual attention literature and the current findings could be due to the task instructions given to participants, with participants instructed to aim for the most luminant object (or the filled white dot in the current experiment which happened to be the most luminant object), and therefore performing the task with a luminance-driven attentional set.

In the perturbed trials of the GO task, the high salience condition resulted in the quickest movement times, the earliest correction times, and the greatest lateral acceleration. The absence of any possible competing stimuli, allowed the motor

system to pick its target and to track it effectively. This result mirrors the findings from Veerman et al. (2008). Although the main result of their study was the distinction between targets identified by luminance, size and orientation and those identified by shape, colour and texture, the control condition in which there were no visible reference objects, produced the steepest lateral acceleration slope, and had the fastest reaction time, in comparison with any of the experimental conditions. The basic double-step task with a simultaneous offset and onset produced the greatest amplitude of corrections in both the current experiment and the Veerman et al. (2008) study. In addition, Brenner and Smeets (2003) also found a greater lateral acceleration, in terms of time and amplitude, for trials when there was only a red target present, as opposed to when the green and red targets were both present and swapped places.

As discussed, the movement times in the GO task under the High Salience condition were shorter than the movement times in the other conditions. In addition to this, the movement times in the High Salience condition were faster when the target was perturbed as opposed to when the target remained stationary. The most likely explanation is that participants were using their right hands to perform an action towards the rightward jump, and this may be more biomechanically comfortable than movements towards the left when using the right hand (Fisk & Goodale, 1985), which is reflected in the movement times and the end point accuracy (see Figure 15). This pattern thus replicates the lateralised patterns observed in the experiments reported in Chapter 2.

Although the effect of salience has been demonstrated in the GO task, in the STOP task there was no effect of condition on the correction time, the stop time or the stop rate. The Low Salience presentation affected movement time performance on the unperturbed trials in both the GO and the STOP, yet failed to have an impact on correction behaviour when the task was to pull the hand back. This could be an effect of power, as there were fewer corrections made in the STOP task, and so less data to drive the analysis. For example, the CT means

are ordered by salience, with the shorter CT for the most salient stimuli, although the differences are not reliable, suggesting that the null effect could be attributed to a lack of power.

An interesting consequence of the chosen design was the presence of placeholders which allowed the manipulation of the salience of the target jump. This poses the question of whether any aspects of the results are influenced, not by the salience of the target jump, but simply by the salience of the placeholder in the target's alternative location. The results from the unperturbed trials suggest that the salience of the placeholder may influence behaviour even when no jump occurs. In the low salience unperturbed trials, the extra object is the most salient of the three salience conditions. In these trials, the movement time to the target is longer than in the other two conditions (with either no other object present, or a one-pixel outline). It appears that the high salience of the other object may have an effect on the movement trajectory even when the target is not perturbed. One possible implication is that the overall lower rates of correction in this design, as compared to the standard double-step tasks in the earlier experiments, may not only be attributable to a reduced salience of the jump even, but also to the presence of a salient object as a potential target in either position, which causes some uncertainty, both in unperturbed and perturbed trials.

The reduced corrections observed in the presence of another potential target cannot fully explain the later corrections towards a colour perturbation. In the Veerman et al. (2008) study, there were reference objects in all of the experimental conditions and the colour stimuli still did not produce as fast, or as many corrections. Also, the probability of predicting the new target location was reduced by having two reference objects and therefore two potential locations, which means that participants were forced to find the new location of the target on the basis of colour information, unlike in earlier studies such as Brenner and Smeets (2004), where participants could monitor the original location for a

change or transient. In both the current experiment and the Brenner and Smeets (2004) study, the presence of the other object in the only other possible target location allowed participants to anticipate a movement to the potential location, and therefore, in principle, they only needed to monitor the original location for a change. The faster corrections reported in the Brenner and Smeets (2004) study might conceivably have been achieved without identifying the new location on the basis of colour (Veerman et al., 2008).

An irrelevant object in the to-be-jumped-to-location does make a potential modification to the trajectory easier to plan. In the current experiment, in the GO task, there was a trend for smaller endpoint errors in the Mid and Low salience conditions compared to the High salience condition, as shown in Figure 15. Additionally, the slower movement times to the Low salience perturbations leads to the conclusion that having the outline in the to-be-jumped-to-location allows the system to plan an alternative movement to that location in advance, but it just takes longer to initiate the alternative plan because the change is less salient. This conclusion receives support from Veerman et al.'s (2008) findings that in conditions where the luminance difference between the target and the reference objects were reduced, there were longer correction latencies to the less salient targets, and more variability in the corrections in trials where the target and the references were similar.

The simultaneous offset and onset of a target between two locations creates the 'jump' in the double-step perturbation paradigm. All the visuomotor studies described above have manipulated at the physical attributes of the stimulus and have used the double-step task to look at the latencies of corrections. Experiment 6 investigates the nature of the double-step aspect of the task, manipulating the form of the target jump itself, rather than just varying the attributes that distinguish the target from the placeholders or references. There was a confound in Experiment 5, as the offset salience and the onset salience were co-varied in order to change the salience of the target jump; their

influences were therefore (intentionally) confounded, making it impossible to distinguish whether the offset and onset events had any independent influences on correction behaviour. Experiment 6 uses similar stimuli to those used in Experiment 5, but independently varies the salience of the onsets and offsets, in order to investigate the separate contributions of each to the power of the jump event to drive corrections. Simply put: is it the onset that captures the hand's correction, or is it the offset that releases the hand to move to the new target location?

Experiment 6: Methods

Participants

Eight adult volunteers (5 females and 3 males, mean age: 19.3 years) took part in the study. The volunteers were recruited using the same procedure as detailed in Experiment 5. All of the participants were right-handed and reported no visual or motor deficits.

Design

The study is made up of four within-participants conditions, each with two manipulated factors (offset salience and onset salience). Using stimuli similar to those used in Experiment 5, the offsets and onsets which make up each 'jump' in the perturbed trials are independently manipulated and differentially weighted using a high and a low salience change. As can be seen in Figure 19, the four perturbed conditions are (1) a high salience offset with a high salience onset, (2) a high salience offset with a low salience onset, (3) a low salience offset with a high salience onset, (4) a low salience offset with a low salience onset. There are also two unperturbed conditions, with the same stimuli presented at T1 and T2,

matching the starting configuration for either the high salience offset conditions, or the low salience offset conditions. As indicated in Figure 19, in the unperturbed trials, the target dot was always presented on the left side and in the perturbed trials, it always jumped from left-to-right.

Each participant performed two blocks of 120 trials each. Within each block, there were 40 trials for each of the two unperturbed conditions, and 10 trials for each of the four perturbed conditions, giving a 33% perturbation rate. Overall, then, there were 80 trials for each unperturbed condition, and 20 trials for each perturbed condition, per participant. The participant was given 20 practice trials before the first block and 10 practice trials given before the start of the second block. As detailed in previous experiments, all stimuli were presented in a random order, a break was given to the participant between blocks and calibration recordings were taken at the end of the second block.

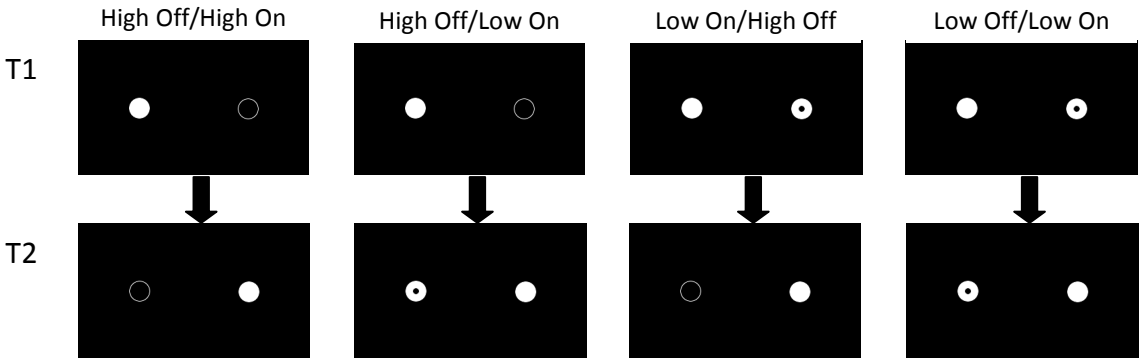
Apparatus and stimuli

The apparatus set up and kinematic recording is the same as described in Experiment 5. The target is a filled white dot presented 35mm to the left of the midline, which stays in the same place in the unperturbed trials and is presented 35mm to the right of the midline in the perturbed trials upon release of the response button.

As can be seen in Figure 19, a high salience onset would involve a one-pixel border being filled in white, to become the target dot, and a high salience offset would involve the filled white dot being replaced with a one-pixel outline. In contrast, the low salience onset would involve the centre of an 11-pixel ring being filled in to create the target dot, and a low salience offset would involve the centre of the target dot being removed, leaving the thick outline behind. In the two unperturbed conditions, the dot and the outline (thin or thick) do not move. In the two salience-same perturbed conditions, the dot and the outline

swap places, and in the two salience-different perturbed conditions, the target dot moves to the right stimulus location and the outline moves to the left, as illustrated in Figure 19.

Figure 19: Perturbed conditions for Experiment 6 (not drawn to scale). The target is the white filled circle, which is always presented on the left of the midline and the 'halo' or outline is always presented on the right. In the perturbed trials, the target appears on the right of the midline upon release of the response button. In the unperturbed trials, the same stimulus is presented for T1 and T2 and so the target does not move. There are unperturbed trials for each of the four conditions with a 33% perturbation rate.



Procedure

The procedure and instructions given to participants are the same as in the GO task in Experiment 5.

Experiment 6: Results

Unperturbed Trials

A paired-samples t-test was performed separately on RT, MT, PV, TPV and AE for the two unperturbed conditions, High salience and Low salience. There was no significant difference between the two conditions for any of the dependent variables [$p \geq 0.302$].

	RT	MT	PV	TPV	AE
High Salience	435.97 (181.88)	408.21 (65.12)	2072.88 (315.28)	129.35 (33.01)	0.40 (1.34)
Low Salience	440.95 (180.60)	411.30 (61.85)	2025.81 (297.33)	131.92 (33.52)	0.36 (1.26)

Table 15: Means for the unperturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets) in the High and Low salience conditions.

Perturbed Trails

Go Condition

As can be seen in Table 16, the majority of perturbed trials in Experiment 6 were classified as corrected at the end of the movement. Therefore, the following analysis is conducted using only the corrected perturbed trials.

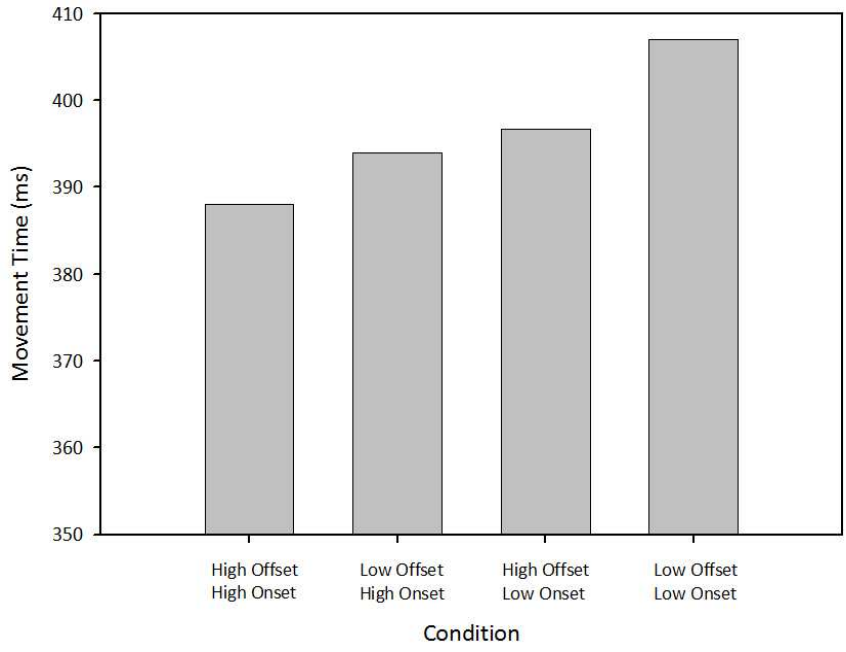
Condition	RT	MT	PV	TPV	AE	Percent Corrected
High Off/High On	441.49 (194.06)	395.16 (51.79)	1999.46 (266.26)	134.80 (35.65)	-0.77 (1.49)	95.51%
High Off/Low On	452.52 (193.29)	405.92 (54.24)	1903.09 (209.05)	137.99 (35.63)	-1.01 (1.42)	87.08%
Low Off/High On	446.78 (192.88)	404.55 (53.15)	1935.63 (260.87)	139.96 (40.95)	-0.68 (1.32)	95.53%
Low Off/Low On	451.10 (198.44)	414.84 (55.74)	1893.60 (244.62)	132.04 (30.69)	-1.05 (1.40)	87.15%

Table 16: Means for the corrected perturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets) in the four Salience conditions. The percent corrected column refers to the percentage of perturbed trials in which the hand was in a corrected position at the end of the movement.

A 2 (offset salience: High, Low) x 2 (onset salience: High, Low) repeated-measures ANOVA was performed separately on MT, PV, TPV and AE. As Figure 20 shows, the shortest movements towards the new target location occur in the High Offset/High Onset condition and the longest movement times occur in the Low Onset/Low Offset condition. There was a main effect of offset salience for

MT [F(1,8) = 12.08; p<0.05], with high salience offsets leading to shorter movement times than low salience offsets, and a main effect of onset salience [F(1,8) = 23.11; p<0.005], with high salience onsets resulting in shorter movement times than low salience onsets. This reduced movement time in the highly-salient onset conditions is mirrored in the peak velocity reached during the movements, with a reliably greater PV reached in the high salience onset conditions compared to the low salience onset conditions [F(1,8) = 11.69; p<0.05]. The salience of the offset or onset of the stimulus perturbation has no effect on the time to reach peak velocity. Taken with the lack of any effect of salience on the unperturbed trials, these findings indicate that the differences between the conditions in the perturbed trials must lie in the latency and/or duration of the corrective part of the movement.

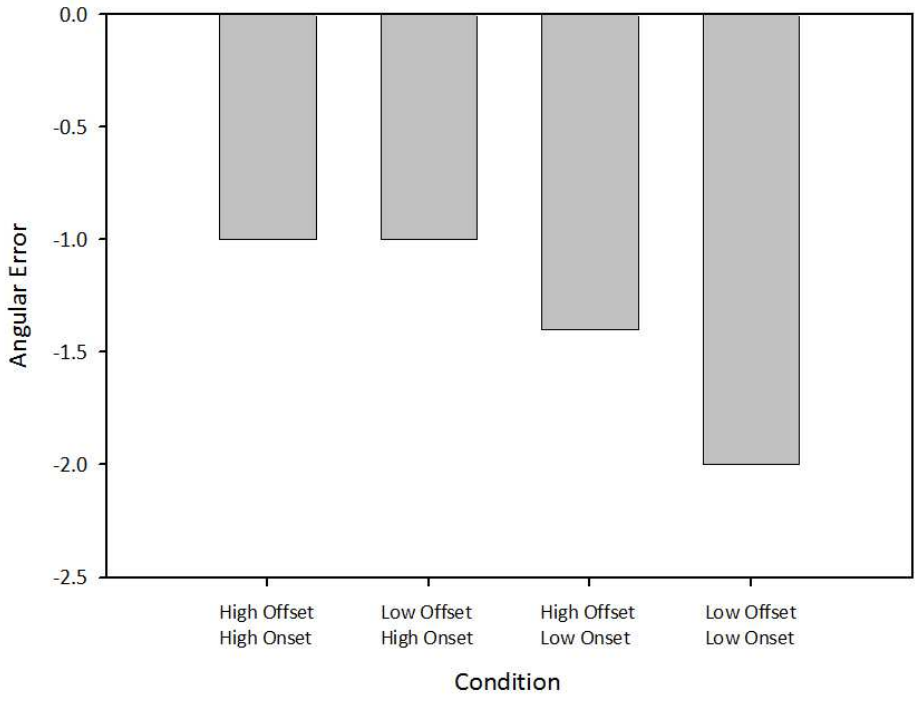
Figure 20: Movement time plotted in milliseconds for the perturbed corrected trials in the four conditions.



As illustrated in Figure 21, corrections were hypometric in all four perturbation conditions (i.e. leftwards AE with respect to the target on the right). There is an effect of onset [F(1,8) = 25.003; p<0.005], with less mean undershoot in the high

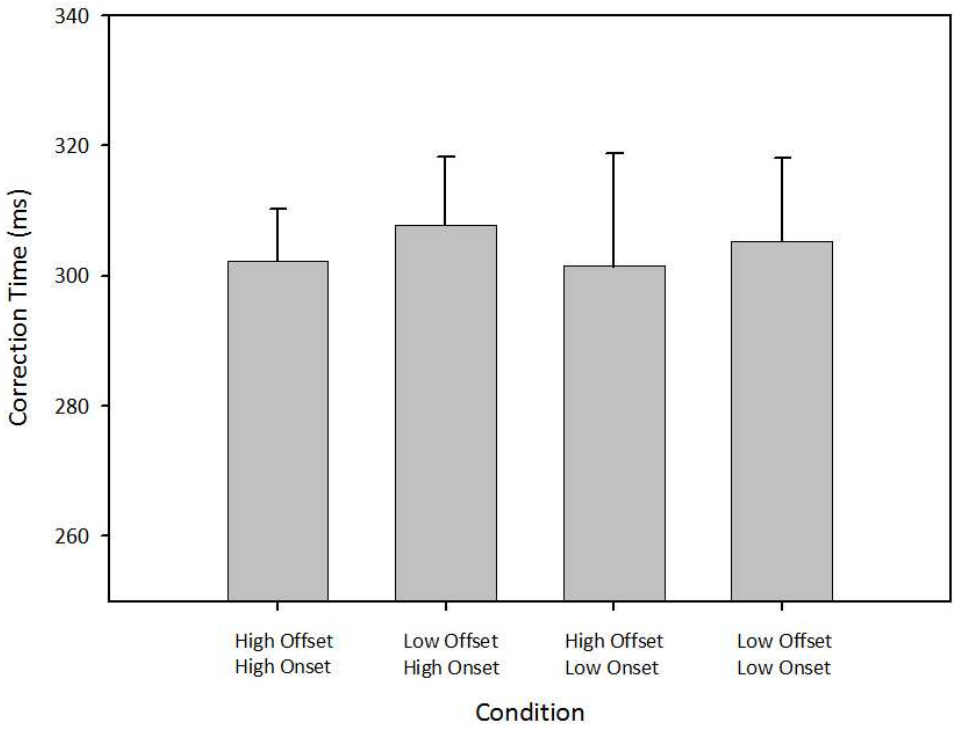
salience onset conditions in comparison with the low onset conditions. These findings contrast with the results of Experiment 5, which demonstrated hypermetric corrections, which overshot the new target location. The differences between the conditions, as observed in Figure 15, were thought to be due to the placeholder in the Mid and Low Salience conditions providing a reference for the to-be-jumped-to location. In the current experiment however, the place-holders do not appear to have the same effect. Instead of being advantageous for correction accuracy, the placeholders in the current experiment make it more difficult for attention to be captured by the new target onset, especially when that onset is of low salience. This potentially differs from Experiment 5, due the difference in the stimuli used. The high salience stimuli in the current experiment are equivalent to the Mid salience stimuli used in Experiment 5, and the low salience change in the current experiment represents a smaller pixel change than the low salience condition in Experiment 5.

Figure 21: AE plotted in degrees for the perturbed corrected trials in the four conditions



An analysis of correction time by condition was performed using perturbed corrected trials, with no reliable effect of salience of offsets or onsets on correction time. Again this result is in contrast with the findings from Experiment 5, and potential explanations are considered in the Discussion section.

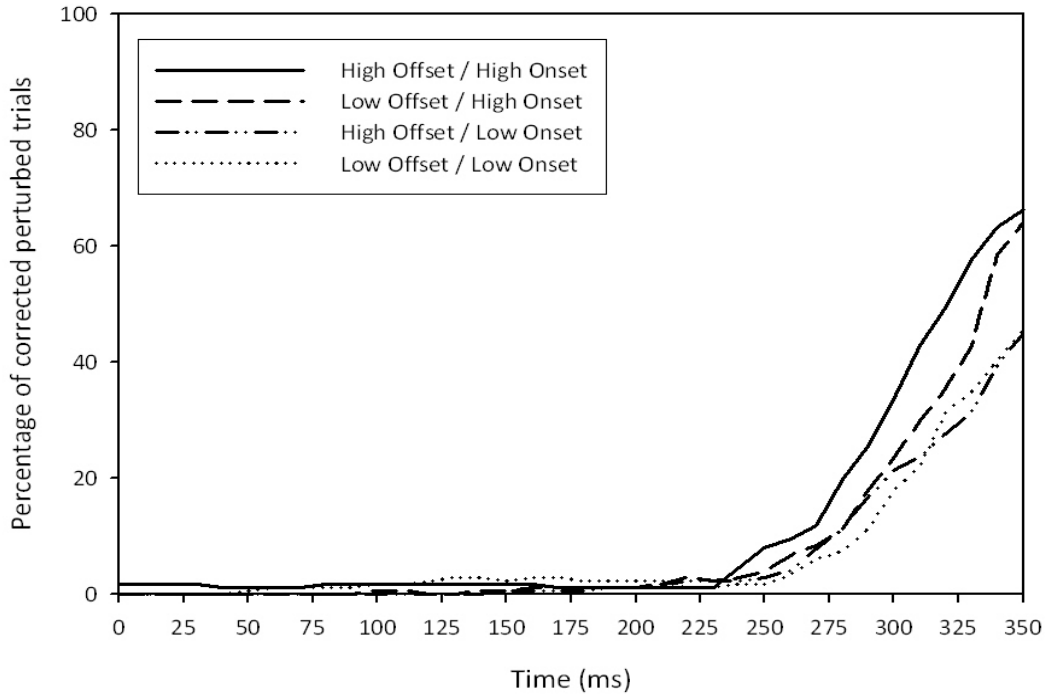
Figure 22: Movement time plotted in milliseconds for the perturbed corrected trials in the four conditions



Individual Corrections

A repeated measures ANOVA was performed on the rate of individual corrections for each 10ms bin up to 350ms (35 levels) by condition. In order for any effect to be considered, it had to remain significant for 50ms. At 290ms, the effect of onset salience becomes reliable [$p \leq 0.035$] with the high salience onset conditions being significantly different from the low salience onset conditions (see Figure 23). The effect of offset salience is not statistically reliable.

Figure 23: The mean rates of individual current corrections for the four conditions, High Offset/High Onset, High Offset/Low Onset, Low Onset/High Offset, Low Onset/Low Offset



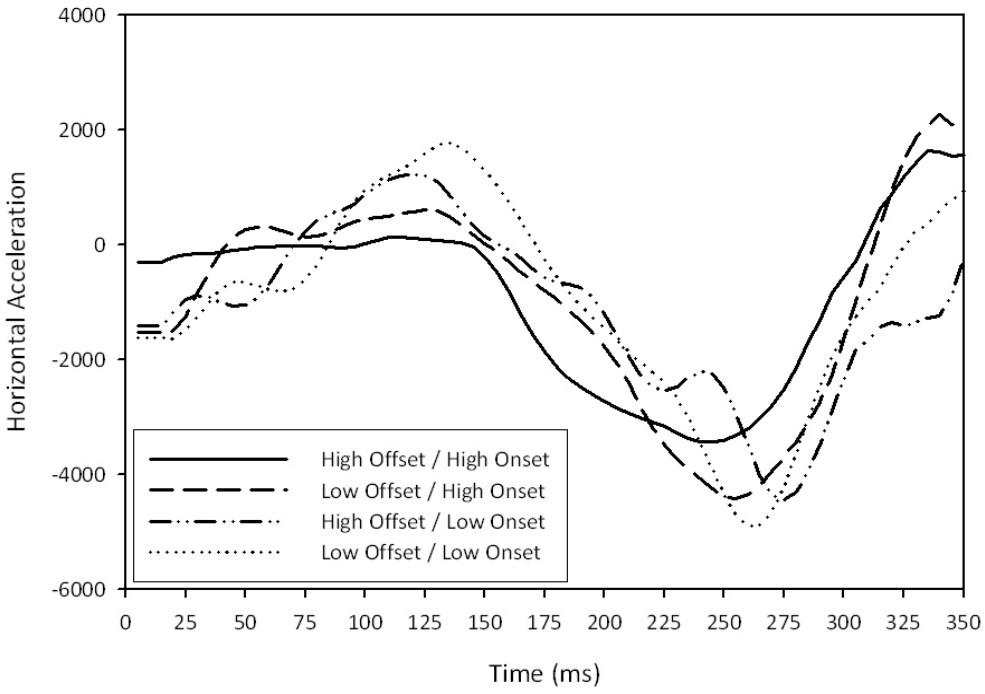
When comparing Figure 23 and Figure 17, it can be seen that the rates of correction are lower in the current experiment, and this is understandable in the light of the findings from Experiment 5. The High salience target in Experiment 5 was presented in isolation, without a placeholder, and resulted in the highest rate of corrections (95.7% at 350ms). The Mid salience condition in Experiment 5 and the High Offset/High Onset condition in the current experiment were equivalent with a one-pixel placeholder also presented, and produced 80.8% corrections in Experiment 5 and 72.1% in the current experiment. The Low salience target in Experiment 5, with the five-pixel placeholder resulted in 67.4% corrections, and then the Low Offset/Low Onset condition, with the 11-pixel placeholder produced 50.5% corrections. The findings from the current experiment concur with those from Experiment 5 in showing that the salience of the jump event reliably affect the rates of corrections produced. However, the present results unpack this further by

demonstrating that the dominant contribution is made by the onset of the new target, rather than the offset of the old.

Horizontal Acceleration Profiles

When the corrected trials from the four perturbation conditions are recoded as a difference from the two corresponding unperturbed conditions, there is no reliable effect of offset or onset salience in the latency of corrections made to the new target location, as can be seen in Figure 24.

Figure 24: The additional lateral acceleration for the perturbed corrected trials in the four perturbation conditions, as a difference from the baseline performance in the corresponding unperturbed trials.



Summary

The clear conclusion to be drawn from this study is that onsets matter most in the context of the double-step task. Movement times are shorter and higher

peak velocities are reached in the high salience onset conditions, than in the low salience onset conditions. The movements in the high salience conditions are more accurate in their endpoints, and rates of corrections towards the new target location are higher, in comparison with the low salience conditions. The CT and the Horizontal Acceleration analysis however, do not show a reliable effect of the salience of the target jump on the time to initiate the corrections.

Experiment 6: Discussion

Onsets appear to matter most to the automatic pilot system, in terms of rates of corrections, yet there is no reliable difference between any of the four conditions in the correction time or horizontal acceleration profiles. Although the movement times were shorter for the High Salience offsets and High Salience onsets, with the shortest being the condition with the combination of the two (see Figure 22), moving faster towards the perturbed target did not result in the correction being made any earlier. The corrections may not have been initiated earlier, but they were more complete in the High Salience onset conditions. The mean end-point errors under all conditions were leftwards, and undershot the new rightward location of the target, but the error produced in the Low offset/Low onset condition was almost twice that of the High offset/High onset condition (see Figure 21).

The end-point errors produced in the current experiment were undershoot, indicating incomplete corrections, yet those produced in Experiment 5 overshot the target location, especially in the High salience condition. The differences between the conditions, as observed in Figure 15, were thought to be due to the placeholder in the Mid and Low Salience conditions providing a reference for the to-be-jumped-to location. In the current experiment however, the place-holders do not appear to have the same effect. Instead of being advantageous for

correction accuracy, the placeholders in the current experiment make it more difficult for attention to be captured by the new target onset, especially when that onset is of low salience. This potentially differs from Experiment 5, due the difference in the stimuli used. The high salience stimuli in the current experiment are equivalent to the Mid salience stimuli used in Experiment 5, and the low salience change in the current experiment represents a smaller pixel change than the low salience condition in Experiment 5.

Although there is a difference in the AE, the correction rates for the equivalent stimuli between Experiment 5 and the current experiment appear to be consistent. As described in the results section, the pattern of results for the correction rates produced are consistent with the amount of visual change occurring as part of the target jump. The condition with the greatest amount of change, the High salience condition in Experiment 5, yielded the highest correction rates. This is then followed by the conditions with the one-pixel, the five-pixel and the 11-pixel placeholders, which produce a pattern of fewer corrections with the smaller amount of change at the new target location.

The fact that there is a smaller amount of change in salience at the new target location across the stimuli in the current experiment may account for the difference in the CT analysis in comparison with Experiment 5. In Experiment 5, there was a reliable difference in the timing of the corrections, with the shortest CT for the most salient target jump, which involved a full offset and a full onset at the new location. This does not occur in the current experiment, as there is always a placeholder present in the to-be-jumped-to-location, and in the Low Salience conditions, this placeholder could be considered a highly salient distractor.

In comparison with Experiment 5, the Low Salience condition presentation did not interfere with unperturbed pointing performance in the current experiment, as there was no difference between the High and Low Salience displays on the

movement characteristics during the unperturbed trials. It may have been expected that the Low Salience stimulus set would have had even more of an effect on baseline pointing behaviour in the current experiment, as the distractor had a border of 11 pixels, in comparison with the five-pixel outline used in Experiment 5.

Within the constraints of the stimulus set used in this experiment, onsets appear to matter most to the automatic pilot system, consistent with the evidence from the visual attention literature reviewed in the Introduction to this section. An abrupt onset produces corrections, with a more salient onset producing higher rates of correction and more complete and accurate corrections. In addition to the High Salience onset helping to drive the hand towards the new target location, this experiment has revealed that a high salience offset may also help the hand to move towards the new target location, either by making the new target easier to identify (as there is less of the old target left behind), or by reducing the attentional pull of the remaining object. Both these factors contribute to a stronger impression of a target 'jump'.

The High Salience offset and onset were the stimuli in the current experiment that most closely approximated a true target jump, as there was not a full offset and full onset condition. In addition to the lack of a full offset and onset, each of the target jumps in the current experiment, and indeed in all of the experiments so far in this thesis, have always had both events (offset and onset) occurring on each perturbed trial. The simultaneous offset and onset produces a change in the visual array that is made up of two events, and it may be that they interact in ways that so far have not been studied. For one to claim that onsets matter most, it must be demonstrated that full onsets are more important to the automatic pilot system than full offsets. In order to determine this, it is necessary to remove the 'jump', and to isolate the elements that usually occur simultaneously. Experiment 7 investigates how the automatic pilot responds when there is only one event: a single offset or a single onset. In order to resolve

any instructional difficulties, Experiment 7 was conducted using the STOP task instruction. It may have been confusing for participants to know which target to point to when there were two identical targets on the screen at once, for example, when there is an additional onset at T2, and thus, the STOP instruction allows the investigation of the effect of the second stimulus, without the need to explicitly state which target to point towards.

Experiment 7: Methods

Participants

Nine adult volunteers (5 females and 4 males, mean age: 18.5 years, SD: 1.13) took part in the study. The volunteers were recruited using the same procedure as detailed in Experiment 5. All of the participants were right-handed and reported no visual or motor deficits.

Design

The study was made up of three within-participants conditions: one condition with a simultaneous offset and onset (standard jump condition equivalent to high salience in Experiment 5), one condition with only an onset and one condition with only an offset. This created two unperturbed stimulus displays, one with a single dot and one with two dots. Each condition consisted of 60 trials, with a 33% perturbation rate. There were two stimulus presentation locations, 35mm to the left and 35mm to the right of the centre of the screen. In the unperturbed trials, the target dot was always presented on the left side and in the perturbed trials, the target dot jumped from left-to-right.

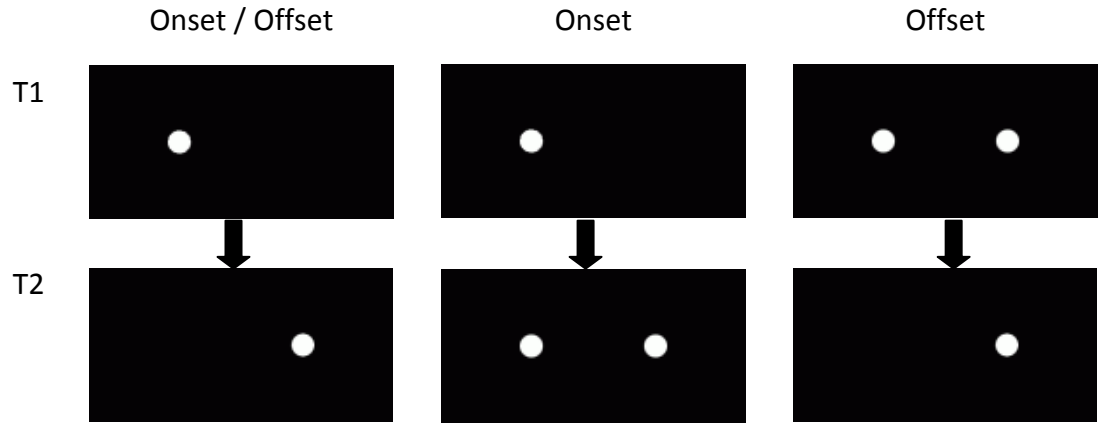
The stimuli were presented in one block of 180 trials, under the STOP instruction. The participant was given 20 practice trials before the experimental block and all stimuli were presented in a random order. At the end of the block, calibration trials were recorded.

Apparatus and stimuli

The apparatus set up and kinematic recording is the same as described in Experiment 5.

Figure 25 demonstrates the three perturbation conditions, with the simultaneous onset and offset, the additional onset of a dot in the right location, and the offset of the dot in the left location upon button release, when the T2 stimulus is presented.

Figure 25: Example stimuli of perturbed trials from Experiment 7 (not drawn to scale). The target is the white filled circle, which is always presented on the left of the midline. In the unperturbed trials, the T1 stimulus is presented in the T1 and T2 positions and so the target does not move. There are unperturbed trials for each of the three conditions with a 33% perturbation rate. In the perturbed trials, the target appears on the right of the midline upon release of the response button.



Procedure

The procedure and instructions given to participants are the same as in the STOP task described in Experiment 5. The participants were additionally instructed that the target dot might jump, a new dot may appear or the dot they were heading for may disappear, but it was emphasised that their job was to head for the target on the left and to pull their hand back immediately when they saw *anything* change on the screen.

Experiment 7: Results

Unperturbed Trials

A paired-samples t-test was performed separately on RT, MT, PV, TPV and AE, for the two baseline conditions, single dot and double dot. There was no significant difference between the two conditions in the unperturbed trials for any of the dependent variables [$p \geq 0.166$].

	RT	MT	PV	TPV	AE
Single dot	468.7 (252.2)	420.6 (54.6)	2062.1 (286.6)	137.3 (40.8)	0.8 (0.7)
Double dot	471.7 (309.3)	419.5 (54.9)	2077.0 (289.4)	134.6 (39.5)	0.8 (0.8)

Table 17: Means for the unperturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets) in the Single dot and Double dot conditions.

Perturbed Trials

Stop Condition

The descriptive data for the perturbed STOP trials is listed in Table 18.

		RT	MT	PV	TPV	AE	CT
Uncorrected Trials	Offset/Onset	438.1 (214.5)	356.5 (62.7)	2050.4 (291.8)	135.3 (37.8)	-7.3 (1.5)	217.3 (113.6)
	Onset Only	453.8 (223.4)	407.0 (62.4)	2110.1 (310.9)	131.2 (36.3)	-7.5 (1.1)	236.0 (120.3)
	Offset Only	493.0 (266.1)	371.3 (56.9)	2047.9 (296.4)	135.5 (37.3)	-7.5 (1.7)	235.8 (139.5)
Corrected Trials	Offset/Onset	605.5 (369.3)	385.6 (41.7)	2090.5 (263.1)	129.1 (32.2)	-4.1 (1.9)	285.5 (50.1)
	Onset Only	490.3 (144.8)	441.7 (82.1)	2081.3 (349.9)	144.2 (37.9)	-3.4 (2.9)	314.3 (114.8)
	Offset Only	375.7 (294.8)	425.5 (82.2)	2119.3 (336.7)	151.0 (97.1)	-3.8 (2.9)	331.4 (77.0)

Table 18: Means for the perturbed trials for each of the dependent variables RT, MT, PV, TPV, AE and CT (standard deviations given in brackets) in the Offset/Onset, Onset Only, and Offset Only conditions.

As can be seen from Table 19, there are very few corrected perturbed trials available for analysis in the Onset Only and Offset Only conditions, and also in the Offset/Onset condition, except for Participant 5. Out of the 20 trials of each condition, participants were correcting on an average of 19.5% trials in the Offset/Onset condition, 3.5% trials in the Onset Only condition and 6.2% trials in the Offset Only condition. There are not enough corrected trials in the three conditions to support an analysis on any of the dependent variables (RT, MT, PV, TPV, AE and CT). For illustrative purposes, however, Table 18 provides the means and standard deviations for these variables, for all of the perturbed trials.

Participant	Offset/Onset	Onset Only	Offset Only
1	10.5	0.0	0.0
2	20.0	10.0	10.0
3	10.0	5.0	0.0
4	10.0	0.0	0.0
5	60.0	10.0	5.0
6	20.0	0.0	0.0
7	0.0	5.9	6.7
8	20.0	0.0	9.5
9	21.4	0.0	30.8
TOTAL	19.5	3.5	6.2

Table 19: The percentage of perturbed trials in which the hand was in a corrected position before the hand was pulled back, for each of the three perturbation conditions.

Although participants did not tend to correct towards the new target location before interrupting their movements, they were able to follow the task instructions and on a high percentage of trials were able to interrupt their ongoing movement in response to the target perturbation, see Table 20.

Variable	Offset/Onset	Onset Only	Offset Only
Stop time	362.9 (48.4)	394.6 (43.8)	365.7 (41.2)
Stop rate	91.0%	55.9%	91.1%

Table 20: Mean stop time in corrected and stopped perturbed trials (ms) and percentage stop rate in corrected perturbed trials. (Standard deviations given in brackets).

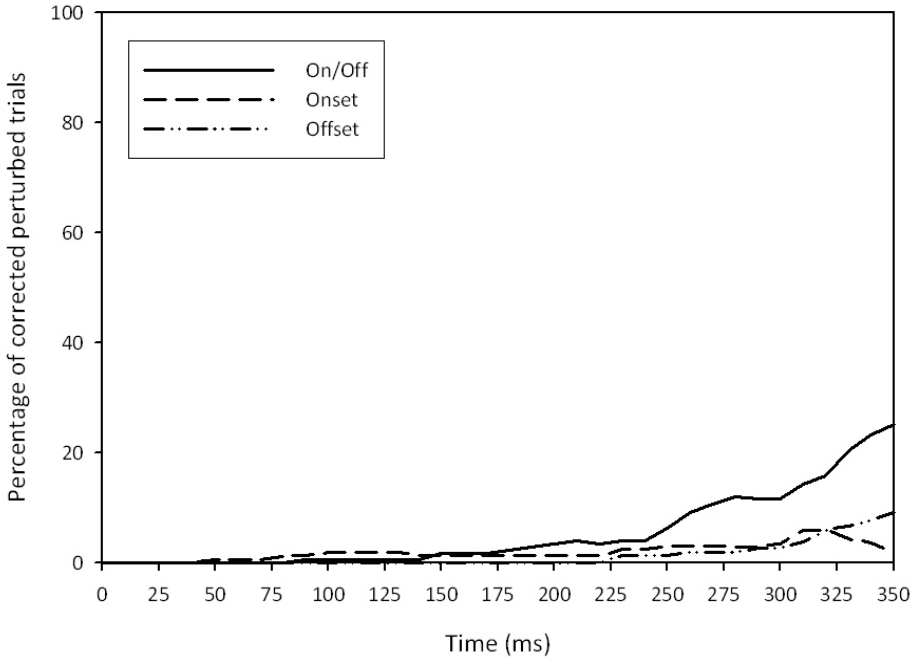
An analysis of Stop time by condition reveals that the Onset Only condition is statistically different from the Offset/Onset condition and the Offset Only condition [$F(2,16) = 6.152$; $p<0.05$], with the Onset Only condition resulting in significantly longer stop times. In addition, there is a statistically reliable difference between the three conditions [$F(2,16) = 13.635$; $p<0.001$] in the

ability to stop the movement in the event of target perturbation, with the Onset Only condition having a lower stop rate than the other two conditions. These results show that participants find it harder to stop their movements in response to a single onset, and when they are able to stop, it takes them longer to do so, the possible reasons for which will be considered in the discussion.

Individual Corrections

As already demonstrated in Table 18, very few of the perturbed trials were classed as corrected for the kinematic analysis. Figure 26 confirms the finding that there were very few corrections made towards the new stimulus location under the STOP task instructions in this experiment. A repeated measures ANOVA revealed that there is no difference between the conditions in the rates of corrections produced. This finding fits with the other results for the current experiment, but appears inconsistent with the findings from previous experiments reported so far. The Offset/Onset condition is almost identical to the original STOP condition in Experiment 1, with the exception of the single direction of target perturbation, yet the rates of correction are much lower. This would suggest that there is something within the current experiment that is affecting performance, and possibly it is the instructions given to participants. This issue is further addressed in the Discussion.

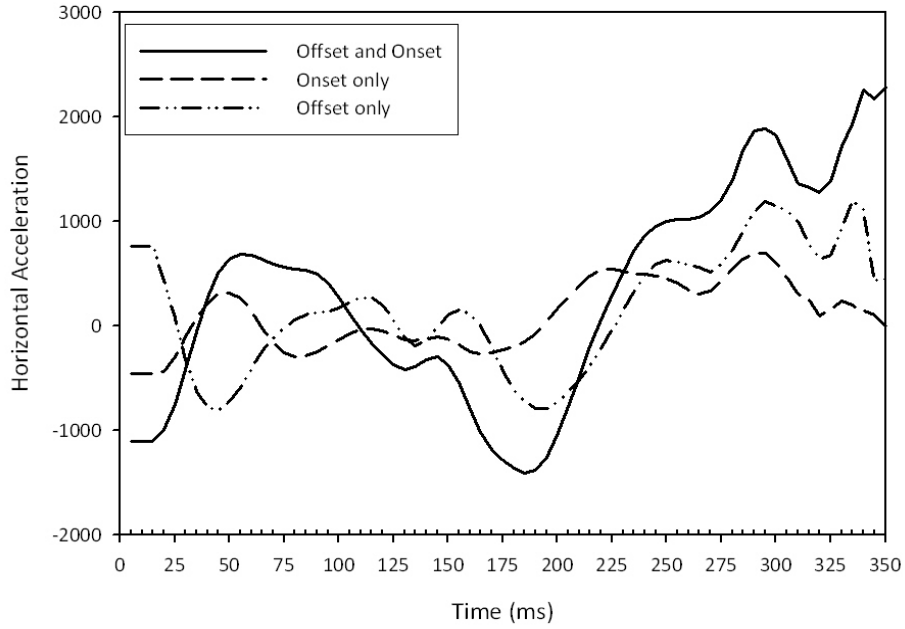
Figure 26: The mean rates of individual current corrections for the three conditions, in the STOP task



Horizontal Acceleration Profiles

There were no differences between the conditions in the in the rates of lateral acceleration, as can be seen in Figure 27.

Figure 27: The mean rates of horizontal acceleration for the three conditions, as a difference from baseline, in the STOP task.



Summary

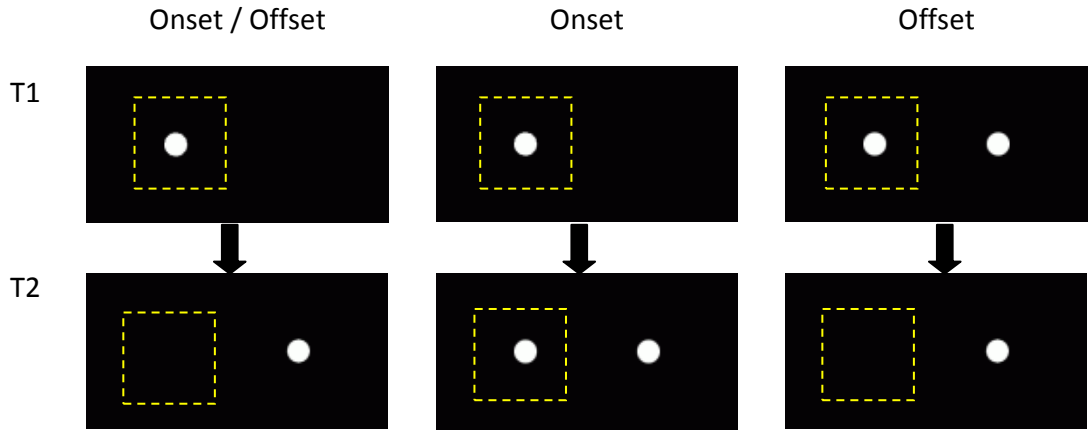
There were very few corrections made to target perturbations in this experiment, as can be seen in Table 19 and Figures 26 and 27. This could perhaps be attributed to the instructions given to the participants. The instruction to always point to the target on the left may have implicitly suggested that participants monitor only the left-sided target position, resulting in fewer corrections being made to towards the new target location on the right. Alternatively, the instruction always to point to the left target may have been interpreted by participants as an 'implicit' NOGO instruction, thereby leading to the suppression of corrections in response to the target perturbation.

Experiment 7: Discussion

There were very few corrections made towards the new target location before the movement was interrupted, in the current experiment. The reason for this could be the instructions given to participants. The instruction to always point to the target in the left may have implicitly produced a level of performance similar to that in the NOGO task, with participants monitoring only the left sided target position. This assumption can also be interpreted as evidence for the dominance of the attentional set, with onsets failing to capture attention. Participants may have selected a strategy to monitor only the left-sided target location, as they were instructed to point to the target on the left and pull their hands back if there was any change. As Figure 28 demonstrates, this strategy could explain the poorer performance in the Onset Only condition, which produced significantly less successful stop rates and slower stop times. If the participant had chosen to restrict his or her attention to the region around the left target location (indicated in Figure 28 by the yellow dashed boxes), then in the Offset/Onset, and Offset Only conditions, this change would be noticed,

whereas the onset in the Onset Only condition may not grab attention, as it is outside the region of interest.

Figure 28: The three perturbed conditions. The yellow boxes demonstrate the to-be-attended-to location. In the Offset/Onset and Offset Only conditions there is a change within the attended region. In the Onset only condition, the change occurs outside of this region, and therefore it takes longer for the change to be detected.



The onset of an extraneous stimulus when another identical stimulus is already present may not be particularly salient, especially if this onset occurs at an unattended location. This pattern of behaviour echoes the results from the Yantis and Jonides (1990) and Theeuwes (1991) studies discussed in the introduction. When attention is already focused on a particular location, whether by a pre-cue arrow or by a rigid task instruction, an abrupt onset in the visual scene outside of that location will fail to capture attention. As well as replicating the findings of Yantis and Jonides (1990) and Theeuwes (1991), this finding also demonstrates that target identity is important to the automatic pilot. Why would the automatic pilot care about the onset of a new stimulus when the original target is still present? The original target has not been displaced, so why should the hand deviate in any way? The unperturbed trials provide a control for any argument that claims that there could have been uncertainty as to which target to head for, when performance in the

unperturbed trials was identical whether there were one or two targets presented. This should also have not been an issue in the perturbed trials either, as this experiment employed the STOP task and the participants did not have to make a decision as to which target to go for if the target moved or changed, as they were instructed to pull their hands back. If the automatic pilot had been interested in the new stimulus onset, then the hand would have deviated towards the new stimulus before the movement was interrupted, as clearly demonstrated in Experiment 1.

The current experiment may also support evidence for enhanced perceptual detection at the attended location. The offsets in the Offset/Onset and Offset Only conditions may have been more effectively detected because they occurred at the location that the participant was intending to move towards (see Figure 28). The Visual Attention Model (VAM: Schneider, 1995) suggests that the visual information selected for visual perception and the visual information selected for the guidance of action are coupled to the common target object, during the execution of a goal-driven task. Evidence for this model comes from the coupling of perceptual and action processes in the programming of saccades (Schneider & Deubel, 1995; Deubel & Schneider, 1996) and the programming of hand movements (Deubel, Schneider & Paprotta, 1998). Participants were better at a perceptual discrimination task when they were concurrently preparing an action to the same object, with performance falling to chance level when the discrimination target was only one degree away from the action target. Following this argument, the detection as indexed by stop time and stop rate of the onset in the Onset Only condition is slower because the change happens in an area of the visual field that has not been selected as a location for a potential action.

Although target location may have received enhanced perception due to the planning of an action to that location, the task performance in this experiment was not enhanced. The Offset/Onset condition in this experiment and the High

Salience condition in Experiment 5 were made up of identical stimuli and participants were instructed in the STOP task in both experiments. Yet, in Experiment 5, participants produced an average correction rate of ~45%, a similar rate to that also produced in Experiment 1, and in the current experiment, the correction rate was ~25%. As already discussed, the instructions given to participants seem to have dampened down the automatic pilot correction performance, even on the most salient of perturbations in the double-step task. These instructions were necessary to instruct participants which stimulus dot was the target for their initial reach. The current experiment could also only be run using the STOP task instruction, because the GO task instructions would have been even more complicated. Specifically, it would have been necessary to instruct participants to do something like the following: point to the target on the left, but if another target appears on the right, then point to that, or if the target on the left disappears, then point to any target that remains. Clearly, these instructions would have been too complex for participants to meaningfully follow.

It was therefore necessary to develop a method of differentially identifying the target and the distractor, without specifying location information. As noted earlier, the automatic pilot does not respond rapidly to colour, and it has already been established that colour as a single property cannot drive fast automatic corrections (Pisella et al., 2000; Brenner & Smeets, 2003; Cressman et al., 2006). If the automatic pilot does not respond to colour, then it may be possible to use colour to distinguish the target from the distractor for instructing the participants, without interfering with the early automatic (location-based) responses of the automatic pilot system.

Experiment 8 is a replication of Experiment 7, but with the addition of small coloured crosses presented in the centre of the target and distractor stimuli. This allows the target to be identified perceptually, without the need for the troublesome STOP instruction employed in Experiment 7. The coloured crosses

enable the experiment to be conducted using the GO task instruction. The target is identified by a green central cross and the distractor is identified by a red central cross. This colour information will allow the participants to plan their initial movement towards the correct stimulus, but if the target is perturbed, it is understood from the literature that the colour will not aid the correction of the trajectory. Experiment 8 also includes a colour control condition, in which the central crosses swap colour, to check that participants are indeed unable to initiate fast corrections on the basis of the colour information alone.

Experiment 8: Methods

Participants

Eight adult volunteers (5 females and 3 males, mean age: 19.3 years) took part in the study. The volunteers were recruited using the same procedure as detailed in Experiment 5. All of the participants were right-handed and reported no visual or motor deficits.

Design

The study is made up of four within-participant perturbation conditions: an Offset/Onset condition, an Offset Only condition, an Onset Only condition, and a Colour Control condition. There were two possible T1 presentations, a single white circle with a green cross, or two white circles, one with a green cross and one with a red cross, and for each T1 stimulus, there were three possible T2 presentations. This resulted in two unperturbed conditions (single dot with a green cross and two dots with green and red crosses), a simultaneous offset and

onset perturbed condition, an offset condition, an onset condition, and a colour control condition.

The stimuli are identical to those used in the previous experiment, with the additional employment of coloured crosses to help identify the target dot, and an extra control condition. In using the green cross to identify the target, it is possible to direct participants to aim for the left-sided target, without giving them explicit instructions to do so, and the red cross provides an contrasting control. The colour control condition was introduced in this experiment in order to to ensure that the trajectory corrections are not produced on the basis of colour, as the only change between T1 and T2 in the perturbed trials is the green and red crosses swapping places. In addition, the Colour Control condition helped to keep the unperturbed stimulus presentations balanced, with two conditions having a single target dot in T1 and two conditions presenting two dots in T1.

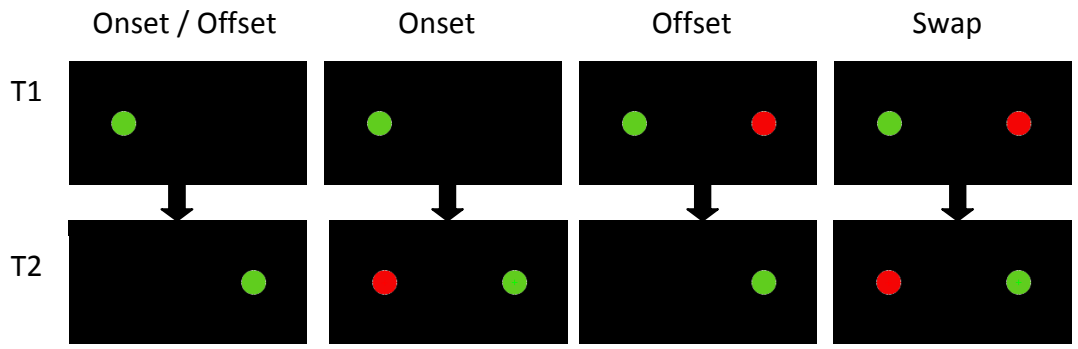
Each participant performed two blocks of 120 trials each. Within each block, there were 40 trials for each of the two unperturbed conditions, and 10 trials for each of the four perturbed conditions, giving a 33% perturbation rate. Overall, then, there were 80 trials for each unperturbed condition, and 20 trials for each perturbed condition, per participant. The participant was given 20 practice trials before the first block and 10 practice trials given before the start of the second block. As detailed in previous experiments, all stimuli were presented in a random order, a break was given to the participant between blocks and calibration recordings were taken at the end of the second block.

Apparatus and stimuli

The apparatus set up and kinematic recording is the same as described in Experiment 5. In addition, the target stimulus was a white dot, 10mm in diameter, with either a green or a red cross (21x21x3 pixels) in the centre.

The two unperturbed and four perturbation conditions are illustrated in Figure 29. The target is the dot with the green cross and the distractor is identified by the red cross. The unperturbed trials either had one white circle with a green cross, presented to the left of the midline or two white circles, one with a green cross and one with a red cross, with the target with the green cross presented to the left of the midline. All dots remained stationary for the duration of the trial. In the perturbation conditions, the white circle with the green cross always started on the left side of the midline in T1 and finished on the right side of the centre in T2.

Figure 29: Example stimuli of perturbed trials from Experiment 8 (not drawn to scale and with coloured dots for clarity). Target is always the white dot with the green cross, which is on the left of the screen in T1 and on the right of the screen in T2 on the perturbed trials. In the unperturbed trials, a single white dot with a green cross, or two white dots, one with a green cross and one with a red cross are presented and remain static on screen after the start button has been released.



Procedure

The procedure was the same as in the GO task detailed in Experiment 5. The instructions differed however, as the participant was instructed to always point to the dot with the green cross in the centre. The participants were additionally instructed that the target dot might jump, a new dot may appear or the dot they were heading for may disappear, but it was emphasised that their job was simply to follow the dot with the green cross wherever it was on the screen.

Experiment 8: Results

Unperturbed Trials

A paired-samples t-test was performed separately on RT, MT, PV, TPV and AE by condition (Single dot, Double dot).

For AE, there is an effect of condition, with greater deviation from the target location in the unperturbed condition when one single target dot was presented, compared to the condition with one target dot and one non-target dot [$t(8) = 3.88$; $p<0.005$]. In both of the unperturbed conditions, the endpoint errors are rightwards. The effect of condition on peak velocity narrowly missed significance [$t(8) = 2.29$; $p=0.051$], with a trend for a greater PV in the single dot condition, compared to the double dot condition. There was also a trend for reaction time to be affected by the presence of the distractor dot [$t(8) = 2.22$; $p=0.058$], with the data suggesting faster RTs to the condition with the single dot presented, implying that participants took time to identify the target in the unperturbed trials when there were two potential targets present. There was no significant difference for MT or TPV between the two conditions in the unperturbed trials [$p\geq0.195$].

Condition	RT	MT	PV	TPV	AE
Single Dot	522.3 (233.7)	423.3 (70.1)	1989.4 (352.3)	129.6 (36.3)	0.4 (0.9)
Double Dot	565.0 (584.7)	426.7 (71.3)	1958.0 (347.5)	134.3 (41.7)	0.5 (1.7)

Table 20: Means for the unperturbed trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets) in the Single dot and Double dot conditions.

Perturbed Trials

Go Task

Participant	Offset/ Onset	Onset	Offset	Colour control
1	100	100	89	95
2	100	94	81	80
3	100	95	5	30
4	45	90	30	75
5	80	90	0	60
6	90	75	75	75
7	100	90	42	84
8	95	90	79	80
9	100	80	70	35
TOTAL	90	89	52	68

Table 21: Percentages of perturbed trials corrected at the end of the movement in the four conditions

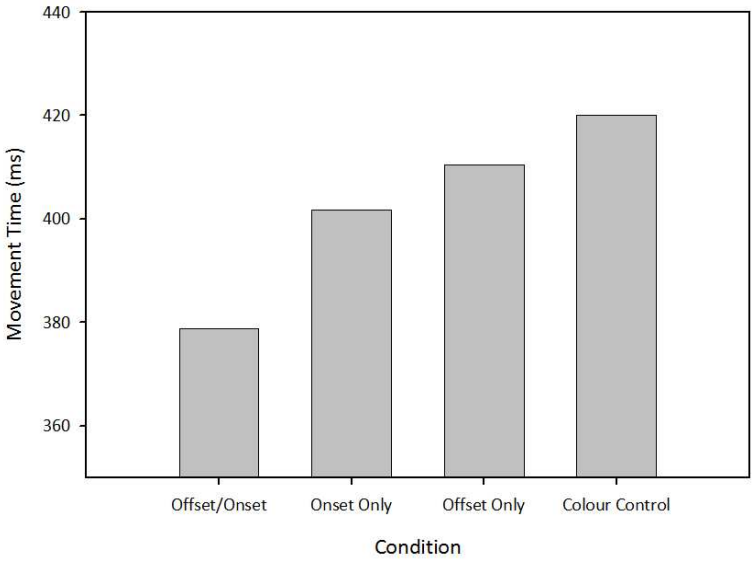
Table 21 lists the percentage of perturbed trials that were corrected in the final frame of the movement for the four perturbed conditions. As can be seen in the table, in the Offset Only condition participant number 5 did not correct on any of the trials, and participant number 3 only corrected in 5% of trials. Participant 3 also failed to correct towards the target in the colour control condition on 70% of trials. Participants 3, 4 and 5 have been excluded from the following analyses on the kinematic features of the movements, as their percentage of perturbed trials that were corrected is below the 35% cut-off, that is considered necessary for inclusion in the analysis.

Condition	RT	MT	PV	TPV	AE
Offset/Onset	564.5 (229.0)	385.0 (63.3)	1983.8 (328.2)	130.8 (39.6)	-0.6 (1.3)
Onset Only	594.6 (223.2)	407.0 (60.4)	1898.0 (309.0)	144.8 (55.6)	-0.8 (1.4)
Offset Only	695.7 (213.1)	411.2 (50.9)	1834.5 (212.1)	140.9 (50.8)	-0.4 (1.1)
Colour control	618.7 (279.3)	425.8 (50.9)	1729.9 (270.1)	145.5 (39.4)	-1.2 (1.6)

Table 22: Means for the perturbed corrected trials for each of the dependent variables RT, MT, PV, TPV and AE (standard deviations given in brackets) in the four perturbed conditions. The data in this table was calculated with Participants 3, 4, and 5 removed.

Due to the fact that there are four perturbed conditions and two baseline conditions, in it not possible to run a condition by perturbation repeated measures ANOVA. Instead, the values for each dependent variable were recalculated as a difference from baseline and a repeated-measures ANOVA was performed separately on MT, PV, and TPV by condition as a difference from baseline (Onset/Offset, Onset only, Offset Only, Colour control swap).

Figure 30: Movement time plotted in milliseconds for the perturbed corrected trials in the four conditions

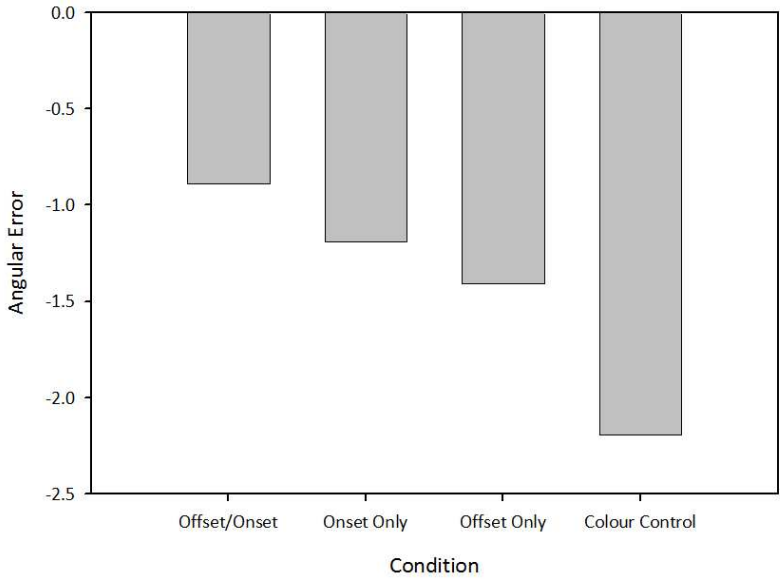


For MT, there was a main effect of condition [$F(3,15) = 4.49$; $p<0.05$], with participants moving significantly faster in the Onset/Offset condition in comparison to the Onset Only condition and the Colour control condition (see Figure 30). There was no reliable effect of condition on the PV or the TPV.

In the unperturbed trials, the target dot is presented on the left of the midline and in the perturbed trials the target is on the right, so calculating the AE as a difference from baseline would be inappropriate, as the endpoints are different. The AE analysis is therefore run using the median endpoint data for each of the four conditions. There is a significant effect of condition [$F(3,15)= 3.34$; $p<0.05$], with the Onset only condition resulting in more accurate movements than the Colour control condition. As can be seen in Figure 31, participants made the

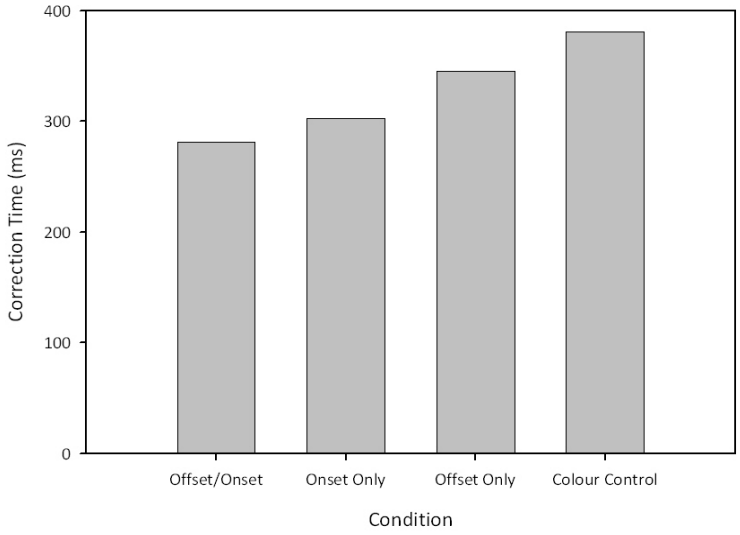
least complete corrections in the Colour control condition, suggesting that the swapping of the crosses inside of the two presented dots was not sufficient for the new target to be identified and for the finger to accurately touch the new target.

Figure 31: AE plotted in degrees for the perturbed corrected trials in the four conditions



An analysis of correction time by condition (Onset/Offset, Onset only, Offset Only, Colour control swap) was performed using perturbed corrected trials, with a reliable effect of condition [$F(3,12) = 11.51$; $p \leq 0.001$]. Figure 32 displays the mean CT for the four conditions, with the Onset/Offset condition having the fastest CT, and participants taking longest to correct in the Colour control condition. The pattern of results is the same when the analysis was rerun with the inclusion of the excluded participants [$F(3,18) = 7.21$; $p < 0.005$].

Figure 32: Mean correction time plotted in milliseconds for the perturbed corrected trials in the four conditions, Offset/Onset, Onset Only, Offset Only and Colour control



Individual Corrections

A repeated measures ANOVA was performed on the rate of individual corrections for each 10ms bin up to 350ms (35 levels) by condition, for all of the participants.

In order for any effect to be considered, it had to remain significant for 50ms (10 consecutive temporal bins). At 240ms, the effect of condition becomes reliable [$p \leq 0.045$], with the On/Off and Offset conditions significantly different to each other and from 280ms, the On/Off and Onset conditions also significantly differ from each other. From 290ms, On/Off and Swap conditions and the Onset and Offset conditions become significantly different to each other, with the Onset and Swap condition statistically reliable by 300ms. The offset and Swap conditions do not statistically differ from each other (in the 0-350ms analysis bin).

Figure 33: The mean rates of individual current corrections for the four conditions, Offset/Onset, Onset Only, Offset Only and Colour control.

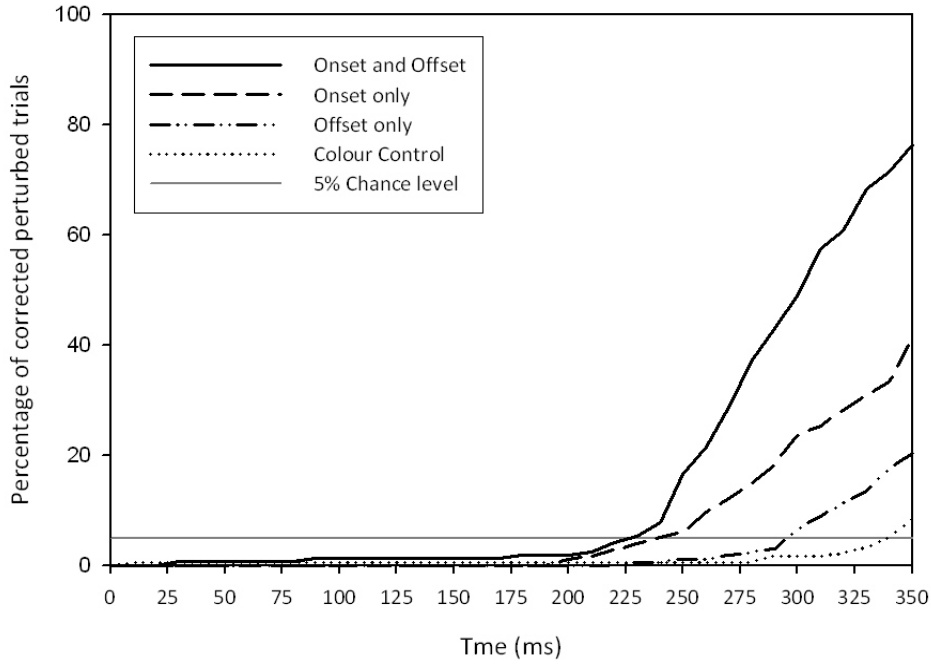


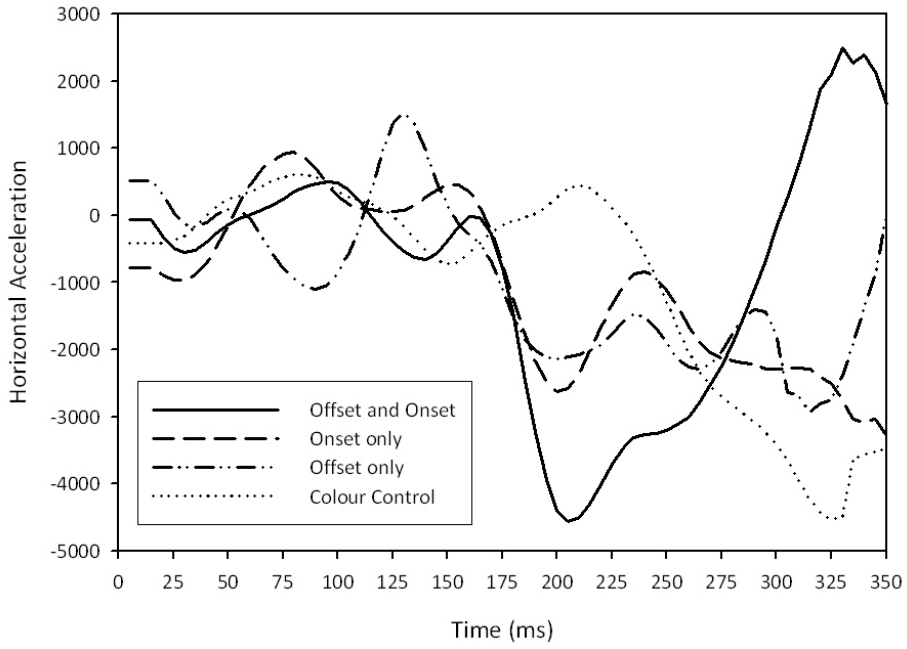
Figure 33 presents the rates of corrections in the corrected perturbed trials. As can be seen, the simultaneous offset and onset results in a higher rate of corrections than a single onset or a single offset. The flat line for the colour control condition provides support for the fact that a colour change cannot elicit fast automatic correction. Only 8% of the perturbed trials were corrected in the Colour control condition, and as can be seen in Figure 33, this small percentages of corrections are occurring very late in the movement. This near-absence of corrections in the colour control condition bolsters the rationale for this aspect of the experimental design, because it implies that (almost) all of the corrections observed in the other conditions were driven by the onsets and offsets of the white dots, not by the location of the green cross.

Horizontal Acceleration Profiles

As with the perturbed trials analysis, the horizontal acceleration repeated measures ANOVA by condition was performed using the recalculated values for the four conditions as the difference from baseline, for all of the participants.

There was a main effect of condition, with the Onset only and Colour Control conditions significantly differing from each other at 185ms, and within the next 5ms, the difference between Onset only and Offset only and Offset/Onset and the Colour control conditions also becomes reliable.

Figure 34: The mean horizontal acceleration profiles, as a difference from baseline, for the Offset/Onset, Onset Only, Offset Only and Colour control conditions.



Summary

There are differences between the two unperturbed conditions in the time taken to initiate the movement, the peak velocity reached during the movement and the accuracy of the endpoint of the movement. The presentation of a single

target dot, in comparison to a target and a distractor dot, tended to produce quicker reaction times and higher peak velocity, but also resulted in larger errors at the end of the movement.

In the perturbed conditions, the simultaneous offset and onset condition produced the highest rate of corrections and the earliest corrections of all the conditions, with these movements towards the new stimulus location being the fastest and the most accurate.

The pattern of results as demonstrated in Figures 30 - 33, suggest that onsets with a simultaneous offset most powerfully drive the automatic pilot, followed by a single onset and then followed by the single offset condition. The colour control condition produced the longest movement times, the latest correction times, and the lowest rate of corrections, indicating that the correction behaviour observed in the other conditions is overwhelmingly driven by the onsets and offsets of the dots, as intended. The colours in the centre of the dots did not drive the effects on the kinematics of the movements or the rates of correction presented here.

Experiment 8: Discussion

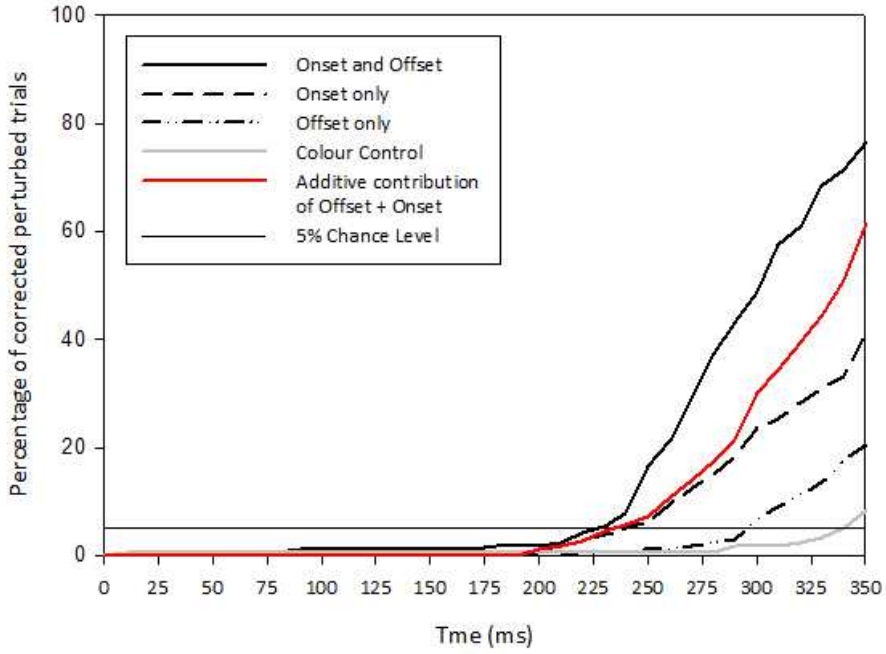
Experiment 8, using a methodological adjustment, was able to answer the question that Experiment 7 failed to settle. The use of coloured crosses provided a successful mechanism to allow participants to identify the target without requiring a complex instruction, yet without interfering with the influence of the target onset and offsets upon correction behaviour. The evidence from the colour control condition supports this claim, with any corrections made to the new target location being fewer, slower and less accurate than in the other conditions (see Figures 30-33). This result is supported by the findings of

Veerman et al. (2008), who demonstrated that participants are still able to correct their movements to targets identified by colour, but at a longer delay. As with visual search paradigms, a coloured target may not grab attention as saliently as an abrupt onset, but the coloured target is identified and found: In the same way, the colour information for target identification can be used by the motor system, but it takes additional time. The delay is likely to have been even more extreme in our design, since the coloured elements of the display were only the small crosses inside larger, brighter white dots.

The main finding of Experiment 8 is that a simultaneous offset and onset is the most powerful event, in terms of the number of corrections made and the timing of those corrections, for the automatic pilot in the double-step paradigm. Figure 33 provides a demonstration of the vast improvement in correction efficiency, when the target appears to 'jump', as opposed to when the elements of the jump are presented individually. Experiment 6 concluded that onsets were the most important element of the jump, yet Experiment 7 revealed that an onset alone is not as effective in attracting attention in the double-step task. The automatic pilot is concerned with tracking the target, and when there is an additional onset, without any change to the original target, the automatic pilot is not interested.

The current experiment demonstrates that the power of onsets to increase correction efficiency, as identified in Experiment 6, is amplified by the occurrence of a simultaneous offset. As illustrated in Figure 35, the individual contributions of the single offset plus the single onset cannot account for the levels of corrections in the Offset/Onset condition. Thus, the 'jump' in the double-step task is understood to be synergistic and produces correction performance that cannot be accounted for by adding the contributions of the offset and the onset together (red line on Figure 35 represents the predicted rate of correction calculated on the basis of making a correction to the onset alone *or* to the offset alone).

Figure 35: The mean rates of individual current corrections for the Offset/Onset, Onset Only, Offset Only and Colour control conditions. In addition, the additive contribution of the Offset Only plus the Onset Only conditions is plotted in red.



A thorough investigation of the reasons behind this synergistic effect is beyond the scope of this thesis, but the visual attention literature suggests two explanations, which may not be mutually exclusive. Firstly, the enhanced power of the target 'jump' could be due to an apparent motion signal which is created with the simultaneous offset and onset of the target. The beta movement, which is produced, is a perceptual illusion during which two still images are combined by the brain to yield a perception of motion (Wertheimer, 1961). This apparent motion could be the trigger for the automatic pilot.

The second possible explanation for the enhanced power of the simultaneous target jump could be that the hand also benefits from a gap effect, just like the eyes. In the eye movement literature, a temporal gap between the offset of the fixation point and the onset of the target stimulus reduces the latency of saccadic responses towards the peripheral target, compared to when the

fixation cross remains on screen (e.g. Bekkering, Pratt & Abrams, 1996). This experimental paradigm is not unlike the double-step paradigm for manual reaching movements, in which the T1 stimulus would act as the initial fixation point and the T2 stimulus would be equivalent to the onset of the target. There have been mixed results in the literature for studies investigating the gap effect for manual aiming movements. Bekkering et al. (1996) demonstrated that the gap effect is evident in manual movements, independent of the occurrence of accompanying eye movements, but only for movements that are goal-oriented. Bekkering et al. (1996) also suggested the involvement of the superior colliculus in the orienting of movements, and it is the offsetting of the T1 stimulus that is understood to release the inhibition of the ocular motoneurons that keep the eyes stationary for the execution of accurate pointing movements (Pratt, et al., 2000). Boulinguez et al. (2001a), however, failed to find a gap effect for the hand, and found that hand movement time and correction latency were shorter in the trials when the T1 stimulus was still on the screen when the movement was initiated. This was in comparison to trials in which the T1 stimulus was presented for only 100ms, and participants were required to point towards a memorised location. The Boulinguez et al. (2001a) experimental set up is different to that employed in current set of experiments in this thesis, and our double-step trials appear to be most similar to the trials that Boulinguez et al. (2001a) consider the no-gap trials. Thus, there is a possibility that a gap effect for the hand could underly, or contribute to, the special power of simultaneous offsets and onsets to trigger online corrections in the present experiments.

General Discussion

Experiments 5 - 8 have explored the properties of the visual target displacement that drive the manual automatic pilot. Experiment 5 manipulated the salience of the target jump, showing that correction efficiency is lawfully related to jump

salience, as would be expected if selection-for-action responds to similar attributes as selection-for-perception. Experiment 6 orthogonally varied the salience of the old target offset and new target onset, demonstrating that online corrections are more strongly dependent upon onset salience than offset salience. Experiment 7, although unsuccessful in breaking down the elements of the 'jump', supported previous findings in the visual attention literature, with onsets in an unattended location failing to capture attention and the attentional set of the participant being paramount in determining which attributes capture attention. Finally, Experiment 8 was able to demonstrate that the onset and offset components of the target jump are synergistic, with the maximum correction rates obtained from a simultaneous offset and onset being greater than that predicted by the additive influences of onsets and offsets occurring in isolation.

In alliance with information that is selected-for-perception, abrupt onsets also have special status amongst information that is selected-for-action for use by the motor system. The power of abrupt onsets however, can be trumped by the simultaneous offsetting of a target from one location and the onsetting of a similar target in a new location. The offset of the old target, it seems, is important in allowing the new target onset to capture attention. This relationship between offsets and onsets is also evident in Theeuwes' (1991) oculomotor paradigm. In trials when the onset occurs before the presentation of the cueing arrow, which pointed reliably to the correct target location, participants were slower to identify the target. The onset of an irrelevant bar in the visual array captures attention and prevents the information from the cue arrow from being used. Similarly, when the automatic pilot is engaged with the original target, it is necessary for that target to offset to free up the attentional resources for efficient 'recapture', as demonstrated in Experiments 6 and 8.

Although abrupt onsets receive prioritised attention in information selected-for-perception and information selected-for-action, an abrupt onset outside of

the current focus of attention does not capture attention. If an abrupt onset captures attention reflexively, then the abrupt onset should override the participant's voluntary allocation of attention to another object. In the experiments published by Yantis and Jonides (1990) and Theeuwes (1991), and in Experiment 7 in the current chapter, this does not appear to be the case. The allocation of attention to an abrupt onset does not appear to satisfy the intentionality criterion, as the attentional set has powerful influence over performance on this task. One interpretation is that once the attentional system driving the automatic pilot is locked-on to a target, as defined by the participant's task set, an onset of an extraneous stimulus is not enough to make it disengage.

Furthermore, the poor performance on the task in Experiment 7 can be interpreted as evidence of the power of intentionality, and provide further support for the role of the task demands in the 'automatic' corrections made by the automatic pilot. The task instructions were designed to make the task as understandable as possible, but it doing so, an important implicit message was overlooked. Instructing participants to always aim for the target on the left and to abort their movements if anything changed could have led to participants monitoring only the left-sided target location and/or could have resulted in an implicit NOGO instruction, impacting on the overall pointing performance. The fact that this strategy could have such an effect on the rates of corrections towards the new stimulus location is further evidence that automatic corrections do not satisfy the intentionality criterion. The intentionality criterion states that the process must not be able to be overridden or stopped by the person's voluntary intentions. Whether the strategy was voluntarily employed remains unknown, but the attentional set and the interpretation of the instructions seems to have strongly suppressed corrections on this task.

As well as replicating findings from the visual attention literature, the results from Experiments 5 - 8 also provide additional support for the identification of

the stimulus attributes that are quick to reach the dorsal stream and are capable of driving online corrections. The results from Experiment 5 replicate those of Veerman et al. (2008), with target salience, as defined by luminance, reliably affecting the rates and amplitudes of the corrections made. The finding that it is the target jump that is of most importance to the automatic pilot makes sense in functional terms, with prioritisation for new objects in the visual field, and for moving objects.

This series of four experiments is able to answer fundamental questions about the attentional aspects of the automatic pilot system. Experiments 5 - 8 have established the importance of particular visual factors in the double-step paradigm, which can be used to drive the automatic pilot, and identified which aspects of the target stimulus and the target perturbation are selected-for-action and used by the motor system. The conclusion to draw would be that attributes and features that are selected-for-perception are essentially the same as the same attributes that are selected-for-action in a double-step task. Furthermore, similar to the findings made in the perceptual attention literature, these bottom-up (exogenous) factors can be powerfully modulated by the participant's (endogenous) attentional set.

There are, however, several questions left unanswered, most notably those generated from the findings of Experiment 8. Further investigation is required into the special power of the simultaneous offset and onset of the stimulus to drive online corrections. Using established findings from the visual attention literature, it may be possible to distinguish whether the simultaneous offset and onset is powerful because it creates an apparent motion signal, or because the hand also benefits from a gap effect, just like the eyes. There are also many other attributes to examine, including the effect of the amplitude and direction of the target jump, as well as the effect of altering the visual similarity of the displaced target to the initial target. In addition, the ability of the automatic pilot to track targets could be teased apart using a paradigm in which the initial

target is replaced by *two* laterally-displaced targets, investigating whether participants are able to suppress automatic corrections under these conditions and, if not, what factors influence the likelihood of selecting one displaced target over the other. Indeed, this suggested 'split-target' task might provide one powerful general paradigm for pitting different target stimuli in direct competition to 'capture' the reaching hand, and thereby to establish which stimulus factors most powerfully drive the automatic pilot.

Chapter Four:

Neurological aspects of the automatic pilot

Outline

Section four addresses the neurological aspects of the autopilot system. The first experiment examines the asymmetry in correction efficiency, which has been evident throughout the earlier experiments, and investigates the role of handedness and hemispheric specialisation. The intention of the following four experiments is to investigate how the automatic pilot system reacts once the substrates of the dorsal stream have been subject to damage. The four single-case studies were designed to test whether the automatic pilot deficit in optic ataxia is simply a manifestation of the more general misreaching deficit.

Experiment 9: Introduction

Handedness is a fundamental human quality and is one of the clearest examples of behavioural lateralisation in humans (Grouios, 2006). The observed differences in the manual abilities of the hands, coupled with the common preference for the right hand led to the investigation of how processes within the brain were distributed. The notion of hemispheric specialisation began as early as with Franz Joseph Gall (1758 – 1828), and developed considerably with the influential findings of Paul Broca (1824–1880) and Carl Wernicke (1848–1905), who demonstrated that identifiable features of language were impaired

following damage to specific regions of the left hemisphere. Further work of John Hughlings Jackson (1835-1911) contributed towards today's understanding that the left hemisphere is responsible for linguistic abilities and the right hemisphere is dominant for visuospatial functions, but it was Hugo Liepmann (1863-1925), a German Neurologist and Psychiatrist, who highlighted the marked asymmetry between the two hemispheres in reference to skilled action, postulating a dominant role for the left hemisphere in the control of movement (see Serrien, Ivry & Swinnen, 2006).

Since then, evidence for left hemispheric specialisation for skilled action has continued to accumulate. The left hemisphere/right hand system was consistently observed to be faster and more accurate over a series of tasks. Carson (1992) attributed the observed superior right hand accuracy and consistency to superior processing in left hemisphere. The early proposal for left hemisphere superiority was that the system was more efficient in correcting errors and making use of sensory information, across a number of tasks that required tapping and aiming movements with constraints on speed and accuracy of performance (Flowers, 1975; Todor & Doane, 1978; Todor & Cisneros, 1985). This became known as the 'feedback processing' hypothesis which proposes that "manual asymmetries are a function of the different efficiencies with which sensory feedback is processed by the hand-hemisphere systems" (Carson, 1992, p.50). The differences between left and right hand performance however, cannot be fully accounted for by the efficiency of visual feedback processing, as differences persist between the two hands when required to point to an illuminated target in the dark (Roy & Elliott, 1986).

As the superiority of the right hand had been observed, there was an assumption that this was related to hand dominance. More recent evidence has demonstrated that although the right hand/left hemisphere system advantage has been established, this is not due to practice with the preferred hand. The contemporary explanation for the right hand advantage is that the left

hemisphere has a specialised role for the control of sequential organisation of complex motor outputs (Fisk & Goodale, 1985; Goodale, 1990), and the right hand is privileged due to direct communication with the left hemisphere.

Many of the earlier findings were conducted with right-handed participants using their dominant hands (Gonzalez et al., 2006), without providing a comparison of the same participants using their left hands. One series of studies that does provide this comparison was conducted by Boulinguez and colleagues (Boulinguez, Nougier & Velay 2001a; Boulinguez, Velay & Nougier, 2001b), who required left and right handed participants to perform tasks with their left and right hands. The first task, investigating movement direction, involved reaching 40cm to a LED target, which was presented in one of five possible locations, and could jump to either the left or the right. In addition, participants also completed a control task in which they were told that there were no perturbed trials and instructed to touch the target as fast as possible.

The right-handed participants moved faster and demonstrated shorter times to correction with their right hands in comparison to their left hands, suggesting that "for right-handers, online movement control is less efficient for the left hand than for the right hand" (Boulinguez et al. 2001a, p.110). Furthermore, for right-handers, the reaction times were longer for movements towards contralateral than for ipsilateral stimuli, demonstrating a need for longer movement preparation time due to interhemispheric transfer (Fisk and Goodale, 1985). One hemisphere receives the information and the other hemisphere produces the response. In addition, contralateral movements were longer than ipsilateral movements in the unperturbed control trials for both the right and left-handed participants, demonstrating the increased biomechanical complexity of contralateral movements

Notably, the possibility of perturbation affected the left and right hands differently, in both left and right-handed participants, lending support to the

idea of a hand/hemisphere specialisation. When there was a chance that the target could be perturbed, the left hand had a longer RT than in the control task, in which the target was always stationary. This finding corresponds with the role of the right hemisphere for motor preparation and action planning (Fisk & Goodale, 1985; Elliott & Chua 1996), resulting in the left hand being more affected than the right hand by a potential target perturbation and the consequential need for on-line correction (Boulinguez et al., 2001a; 2001b).

These experiments demonstrate that manual asymmetries are modulated by different activities, with the right hand/left hemisphere system specialised in temporal processing and correcting movement online, and the left hand/right hemisphere more expert in spatial processing and distance judgements. Boulinguez et al. (2001a) state that handedness is the most obvious example of hemispheric specialisation, and although the right hand advantage for the online directional control of movements was independent of handedness (Boulinguez et al., 2001a; 2001b), this hemispheric advantage is exaggerated in right-handers, who are skilled with their right-hands through practice (Boulinguez et al., 2001b).

The left and right hands have been shown to behave differently in terms of visually guided action, and the online correction of aiming movements, but is there the same hemispheric difference in terms of visual perception? Previous research has shown that action and perception can be dissociated under certain conditions, with the use of visual illusions. In healthy participants, visual illusions have an effect on perception, but little or no effect on grip aperture during grasping (Aglioti et al., 1995; Dewar & Carey, 2006; Haffenden et al., 2001). Thus it has been established that the dorsal stream is insensitive to the lure of the visual illusion, but it is unknown whether there is a difference in susceptibility between the two hands, as previous studies have used right-handed participants using their dominant hand (Gonzalez, Ganel, & Goodale., 2006).

Gonzalez et al. (2006) tested left- and right-handers with their left and right hands in a perceptual illusion task, using the Ponzo and Ebbinghaus illusions. They found no differences in movement time between the hands, but did find that the left hand grip aperture was more affected by the illusions than the right-hand grip aperture, irrespective of handedness. The participants opened their left hand wider for the illusionary larger object and smaller for perceived smaller object, even though both objects were the same size, with the right hand 'perceiving' the real size and the left hand 'perceiving' the apparent size of the object.

In a further, more naturalistic set-up, Gonzalez et al. (2006) required participants to either construct a Disney puzzle or make a model out of Lego. The pieces were randomly distributed across a table top, and the video-taped performance was scored for hand preference for grasping in ipsilateral and contralateral space. The results showed a marked preference for right-handers to use their dominant hand (78%), yet the left-handers displayed no opposite preference, using their right hand 52% of the time. The left-handers were shown to use their non-dominant hand significantly more than right-handers do, in both ipsilateral and contralateral space, and although left-handers do not use their right hands as much as right-handers do, they still show the right hand/left hemisphere advantage for picking up small objects quickly and accurately.

Gonzalez et al., in their 2007 paper, extended the naturalistic task to investigate the reaching component of the prehension movement. Participants had to perform two tasks - complete a 24 piece puzzle and build five models out of 95 Lego pieces - without direct instruction as to which hand to use. A strip of white tape divided the table top in two and the Lego and puzzle pieces were evenly distributed across the two halves of the surface. Participants' performance was videotaped and hand preference was scored by two blind judges.

In the puzzle task, the right-handers picked up puzzle pieces with their right hand 75.9% of the time, preferring to use their right hand in left-sided space. In comparison, left-handers used their dominant left hand only 48.5% of the time. Left-handers used their non-dominant hand much more then the right-handers did. Right-handers rarely used their left hand in right space, but left-handers regularly used their right hand in left space. The same pattern of results was evident in the Lego task, with left- and right-handers using their dominant hands 44.4% and 82.2% of the time, respectively. Gonzalez et al. (2006) reported that left-handers were 20 times more likely, than right-handers, to reach across their body with their non-dominant hand.

In terms of both reaching and grasping, right-handers show strong hand dominance, but left-handers tend to show no hand preference at all. Left-handers were much more likely to use their non-dominant hand than were right handers, even on the opposite side of the table. The overall predominance of right-hand use for visuomotor control lead Gonzalez et al. (2006) to conclude that the left hemisphere is crucial in execution of accurate reaching and grasping, independent of handedness, tying in with ideas from the neuropsychology literature (Perenin & Vighetto, 1988), that the left hemisphere has a special role in visuomotor control.

Experiment 9 sets out to investigate the influence of handedness and hemispheric specialisation for aiming movements in the double-step task. Left- and right-handed participants were required to reach towards a central target, which was perturbed to a new location on the left or right of the screen, with both their left and right hands. If the advantage for right-handed participants, using their right hand to reach to rightward targets, evident in Experiment 1, is due to biomechanical constraints (and/or hand/hemisphere compatibility), then a similar advantage would be afforded to left-handed participants using their left hands to reach towards leftwards jumping targets. However, if the right hand advantage is the result of hemispheric specialisation, above and

beyond handedness, then it would be expected that, on the whole, participants would produce more efficient corrections with their right hand, independent of handedness.

Experiment 9: Methods

Participants

Thirty adult volunteers (11 right-handed females and 4 right-handed males, mean age: 20.6 years, SD: 7.07 and 11 left-handed females and 4 left-handed males, mean age: 20.4 years, SD: 5.98) took part in the study[1]. The majority of these volunteers were recruited amongst the Undergraduate students in the Psychology Department at the University of Edinburgh. The participants were well matched for age, sex and handedness laterality scores (Right-handed: 85.67%, SD: 15.68, Left-handed: -75.21%, SD: 26.05, paired-samples t-test: $t(13)=0.98$; $p=0.35$, as measured by a modified version of the Edinburgh Handedness Inventory: Oldfield, 1971; Cohen, 2008) and reported no visual or motor deficits.

Design

The study consisted of two blocks of 120 trials, one block performed with each hand. Each block was made up of 80 unperturbed trials, 20 trials in which the target jumped to the left and 20 trials in which the target jumped to the right, thus producing a 30% perturbation rate. On all trials, the target was presented in the centre of the screen for the T1 presentation, and either remained stationary when the participant released the button on the unperturbed trials,

[1] With thanks to four undergraduate psychology students who assisted in recruitment and data collection for 16 participants. All undergraduate experimenters were trained and monitored, and followed a strict experimental procedure which was identical for all participants.

or was perturbed 54mm to the left or 54mm to the right on the perturbed trials (T2). All stimuli were presented in a random order and a break was given to the participant between blocks. At the end of each block, eight calibration trials were recorded, with the index finger positioned on the response button, the centre of the screen and 54mm to the left and to the right of the centre to provide reference points for the calculation of spatial error.

Apparatus

The participant sat at a desk with their left hand resting on their lap and their right-hand index finger resting on the start button. Stimuli were presented on a 3M M170 5-wire resistive touchscreen (active display area 340 x 270mm, resolution 1024 x 768 pixels) in front of the participant, with a distance of 505mm from centre of screen to the start button, in a dimly illuminated room. The stimulus was a white dot, 10mm in diameter, presented on a black background to reduce glare. On all trials, the target appeared in the centre of the screen when the button was pressed, and either stayed in its initial position (unperturbed trials) or made a jump to 54 mm to the left or right of the central position (perturbation trials) when the button was released at movement onset.

Electromagnetic tracking equipment (Optotrak: Northern Digital Inc., Waterloo, Ontario, Canada) was used to record the kinematic features of the aiming movement from commencement to cessation at 200Hz for a maximum duration of 1 second. One infrared-emitting diode was secured to the participants' right index finger.

Two tones were used to pace the participant's movements. The first tone was sounded 350ms after movement commencement and participants were instructed to touch the dot on the screen in time with the beep. The second tone was sounded 1000ms after the start of the movement and participants were instructed to return to the start button after the second beep.

Procedure

The participants were instructed in the GO task instruction, as detailed in Experiment 1. Each participant performed the task with both their right and left hands, with the order of the starting hand counterbalanced between participants.

Experiment 9: Results

Unperturbed Trials

Movement characteristics of the unperturbed trials were used to characterise baseline reaching behaviour. The descriptive data from these trials is summarised in Table 23.

A mixed model ANOVA was performed separately on MT, PV, TPV and AE with dominant hand (left, right) as a between subjects factor and acting hand (left, right) as a within subjects factor.

There was a main effect of both dominant hand [$F(1,28) = 7.62$; $p<0.01$] and acting hand [$F(1,28) = 14.96$; $p\leq0.001$] on MT, with right-handed participants producing shorter MTs and participants overall moving faster with their right hand. There was no significant interaction. As well as moving faster, participants acting with their right hand reached a higher PV [$F(1,28) = 45.44$; $p<0.001$], and although there was no reliable effect of acting hand on TPV, hand dominance was reliable [$F(1,28) = 5.263$; $p<0.05$], with right-handed participants quicker to reach PV. There was no effect of hand dominance or the hand used to perform the task on angular error in the unperturbed trials.

Dominant Hand	Acting Hand	MT	PV	TPV	AE
Left	Left	462.6 (49.1)	1850.3 (257.3)	135 (40.9)	0.00 (-0.3)
	Right	435.6 (43.3)	2135.3 (312.6)	124.5 (23.6)	0.2 (-0.2)
Right	Left	418.8 (46.3)	1937.6 (285.7)	110.1 (33.2)	0.1 (-0.2)
	Right	382.1 (70.0)	2326.3 (376.0)	103.1 (24.1)	0.2 (-0.3)

Table 23: Means for the unperturbed trials for each of the dependent variables, MT, PV, TPV, and AE (standard deviations given in brackets). Dominant hand refers to the outcome of the handedness laterality scores and acting hand is the hand used to perform the task.

Perturbed Trials

Table 24 summarises the reaching behaviour in the perturbed trials and shows the percentage of perturbed trials that were in a corrected position in the final frame of the movement. As can be seen, there is a high incidence of corrected trials in the different condition combinations, as would be expected for this standard GO version of the double-step reaching task.

Dominant Hand	Acting Hand	Jump Direction	MT	PV	TPV	DT	AE	Percentage Corrected
Left	Left	Left	463.5 (50.0)	1841.5 (269.5)	139.3 (47.3)	328.03 (47.22)	0.8 (1.4)	83.7
		Right	478.9 (39.9)	1828.3 (246.9)	127.6 (38.4)	351.25 (40.61)	-0.1 (0.8)	81.7
	Right	Left	491.7 (45.3)	2096.0 (284.7)	121.7 (26.6)	370 (36.18)	0.6 (0.9)	82.5
		Right	411.6 (37.1)	2109.7 (298.4)	124.3 (25.0)	291.07 (25.05)	-0.5 (1.0)	84.6
Right	Left	Left	417.6 (44.9)	1957.2 (292.7)	105 (33.4)	312.66 (38.51)	0.5 (0.6)	94.8
		Right	439 (45.1)	1922.6 (264.1)	109.8 (34.0)	329.16 (37.51)	-0.3 (0.6)	90
	Right	Left	442.8 (71.2)	2257.7 (387.0)	104.8 (26.3)	338 (58.37)	1.3 (1.2)	78.9
		Right	356.1 (49.9)	2267.9 (339.0)	109.8 (24.8)	246.33 (38.98)	-1.4 (1.0)	79.3

Table 24: Means for the corrected perturbed trials for each of the dependent variables, MT, PV, TPV, DT (Deceleration time, calculated from the time to reach PV to the end of the movement) and AE (standard deviations given in brackets). The 'percentage corrected' row provides the percentage of perturbed trials classified as corrected at the end of the movement.

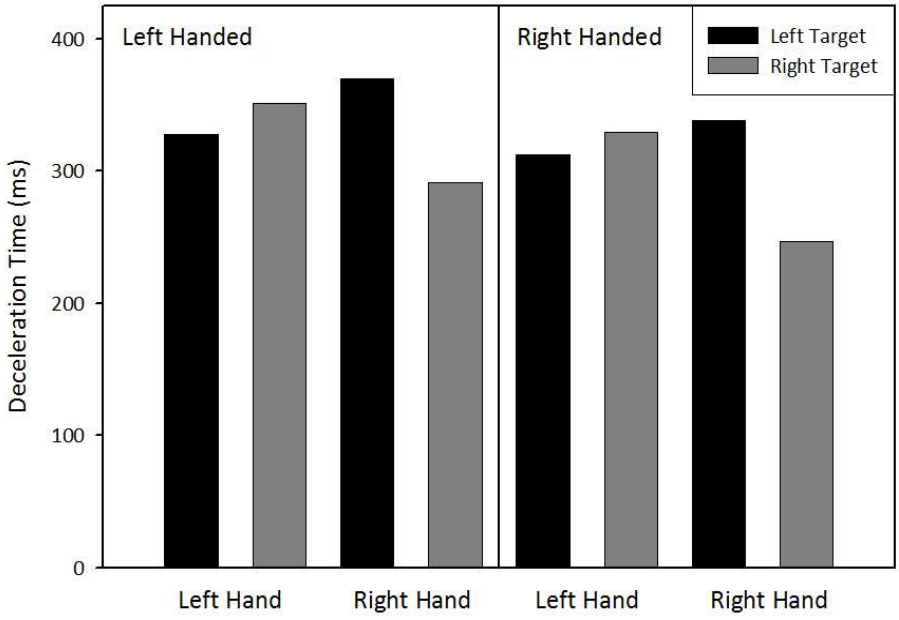
A mixed model ANOVA was performed separately on MT, PV, TPV, DT and AE with dominant hand (left, right) as a between subjects factor and acting hand (left, right) and jump direction (left, right) as the within subjects factors.

For MT there was a main effect of dominant hand [$F(1,27) = 9.42$; $p<0.005$], with the right-handed participants moving quicker than those who were left-handed, as was found in the unperturbed trials. There was also a main effect of the acting hand [$F(1,27) = 11.23$; $p<0.005$], with shorter MT when using the right hand, and a main effect of jump direction [$F(1,27) = 140.76$; $p<0.001$], with quicker movements towards rightward targets. In addition, there was also a

significant acting hand by jump direction interaction [$F(1,27) = 105.87$; $p<0.001$], with the rightwards perturbations resulting in quicker MT when using the right hand. The right hand also reaches a higher PV than the left [$F(1,27) = 39.33$; $p<0.001$].

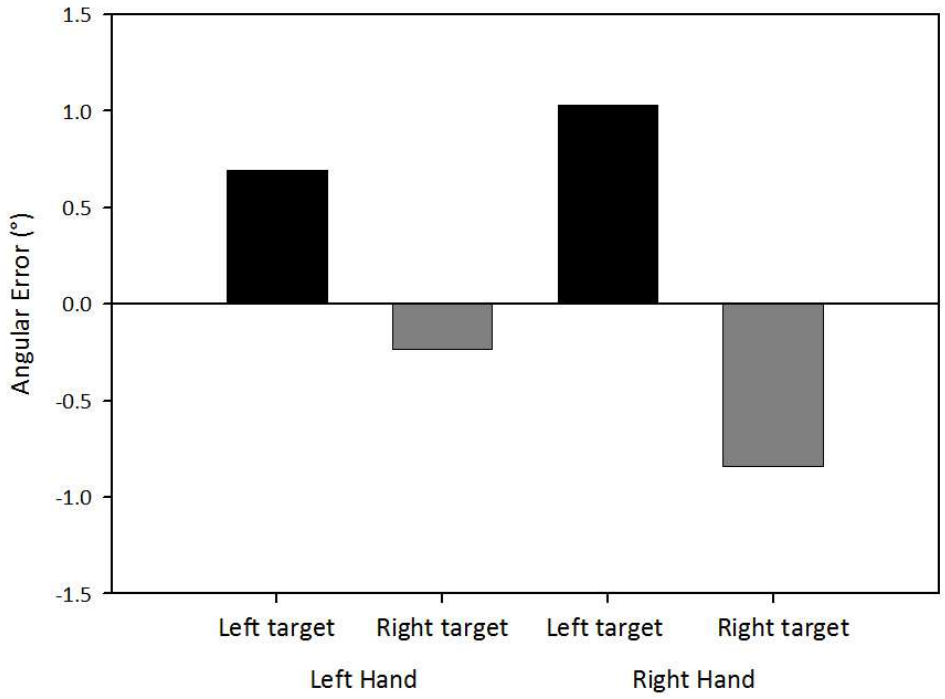
There was no effect of hand dominance, acting hand or perturbation direction on the TPV of the corrected perturbed trials, suggesting that any differences in MT arose in the deceleration phase of the movement. This is supported by the DT analysis, which revealed that there were reliable differences between the dominant hands [$F(1,27) = 5.81$; $p<0.05$], with a shorter DT for the right-handed participants. There is a main effect of acting hand [$F(1,27) = 6.80$; $p<0.05$], and perturbation direction [$F(1,27) = 57.41$; $p<0.001$] on the deceleration phase of the movement, in the context of a highly significant acting hand x side interaction [$F(1,27) = 109.63$; $p<0.001$], with a shorter DT when reaching ipsilaterally, especially when using the right hand to reach towards a rightward jumping target, as can be seen in Figure 36.

Figure 36: The mean deceleration time for the corrected perturbed trials for left- and right-handed participants, using their left and right hands to reach towards left (black bars) and right (grey bars) perturbed targets.



The direction of the perturbation had a significant effect on the accuracy of the end of the movement, with larger errors to leftwards perturbed targets [$F(1,27) = 19.68$; $p<0.001$], however, errors towards rightwards targets increased when using the right hand [acting hand x jump direction interaction: $F(1,27) = 7.23$; $p<0.05$]. As there was no main effect of dominant hand, the data illustrated in Figure 37 has been collapsed across all participants. As can be seen, the corrections towards the T2 targets tended to fall short of the actual target position, and are hypometric in nature for perturbations in both directions and when using either hand.

Figure 37: The angular error of the end point of the movement plotted in degrees for all participants using their left and right hands to correct towards left and right perturbed targets.



The correction time analysis corroborates the pattern of findings for MT. The mixed model ANOVA was performed using the corrected perturbed trials, with dominant hand as the between subjects factor and acting hand and perturbation direction as the within subjects factors. There was a main effect of dominant hand [$F(1,27) = 10.62$; $p<0.005$], acting hand [$F(1,27) = 4.20$; $p<0.05$] and

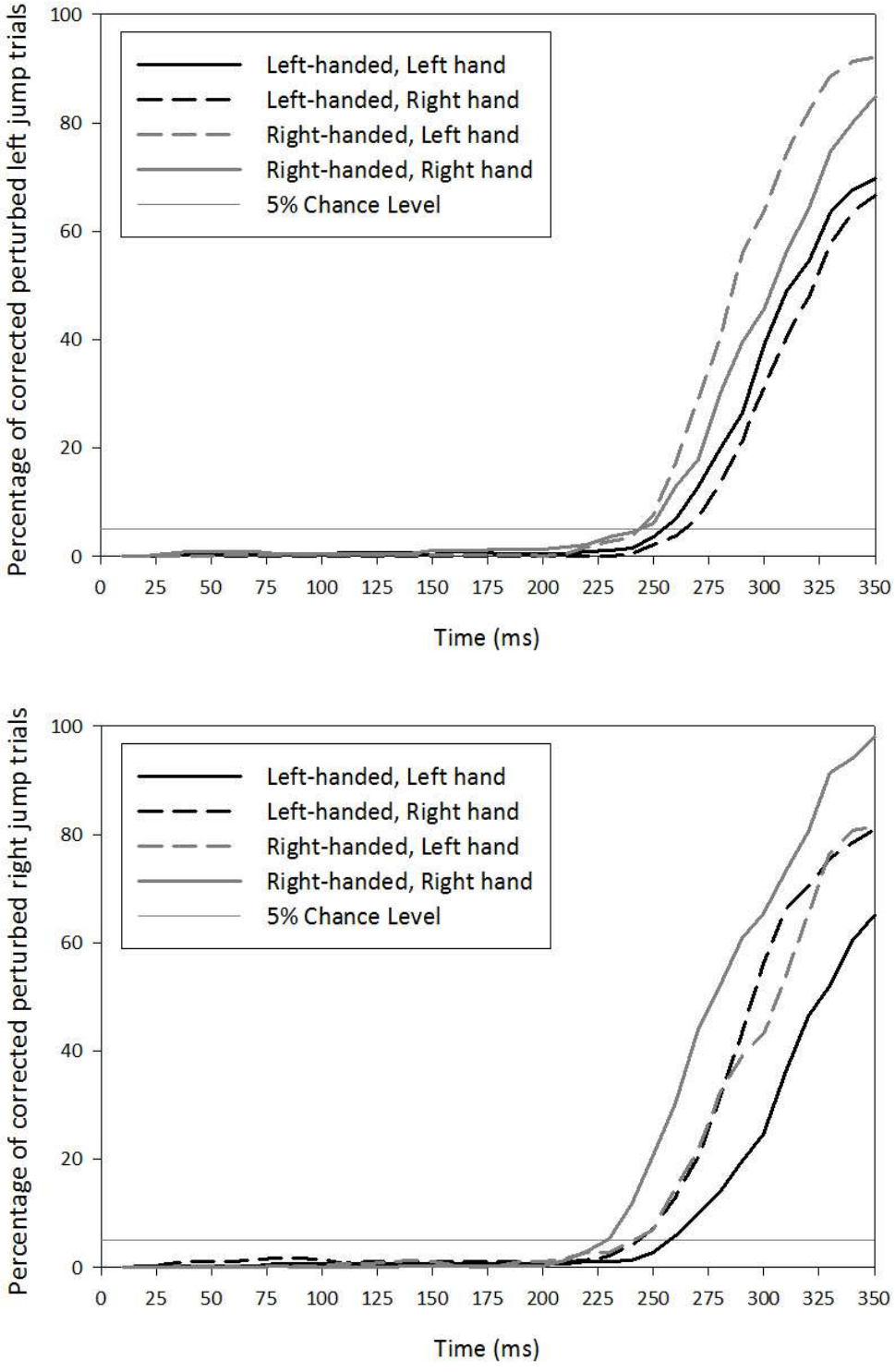
perturbation direction [$F(1,27) = 14.63$; $p<0.001$] on CT, with corrections made by right-handers showing up earlier in the spatial trajectory, in comparison with left-handed participants. The participants had a shorter CT when acting with their right hand, and also when correcting towards a rightwards target. In addition, there was a reliable acting hand x perturbation direction interaction [$F(1,27) = 10.62$; $p<0.005$], with the right hand producing a shorter CT for rightwards targets and the left hand producing a shorter CT for leftwards targets.

Individual Corrections

A mixed-model ANOVA was performed on the rate of individual corrections for each 10ms of the movement up to 350ms, with dominant hand (left, right) as the between subjects factor and acting hand (left, right) and jump direction (left, right) as within subjects factors.

In the previous experiments reported in this thesis, for any effect to be considered, it had to remain significant for 50ms (10 consecutive temporal bins). At 240ms, a jump direction x acting hand interaction becomes reliable [$p\leq0.049$], with more corrections produced to a left jump with the left hand and more corrections produced to a right jump when using the right hand, although the percentage of right hand corrections is considerably more, as can be seen in Figure 38. No other effects were consistent for 50ms, however, there was a reliable effect of hand dominance for 45ms, from 220ms [$p\leq0.016$], with more corrections produced by right-handed participants. Furthermore, there was also a reliable effect of acting hand for 40ms, from 240ms [$p\leq0.044$], with more corrections made when using the right hand, irrespective of handedness.

Figure 38: The mean rates of individual current corrections towards left and right target perturbations, plotted separately. The Left-handed participants are plotted in black lines and the right-handed participants are plotted in grey lines. The dashed lines denote performance with the non-dominant hand



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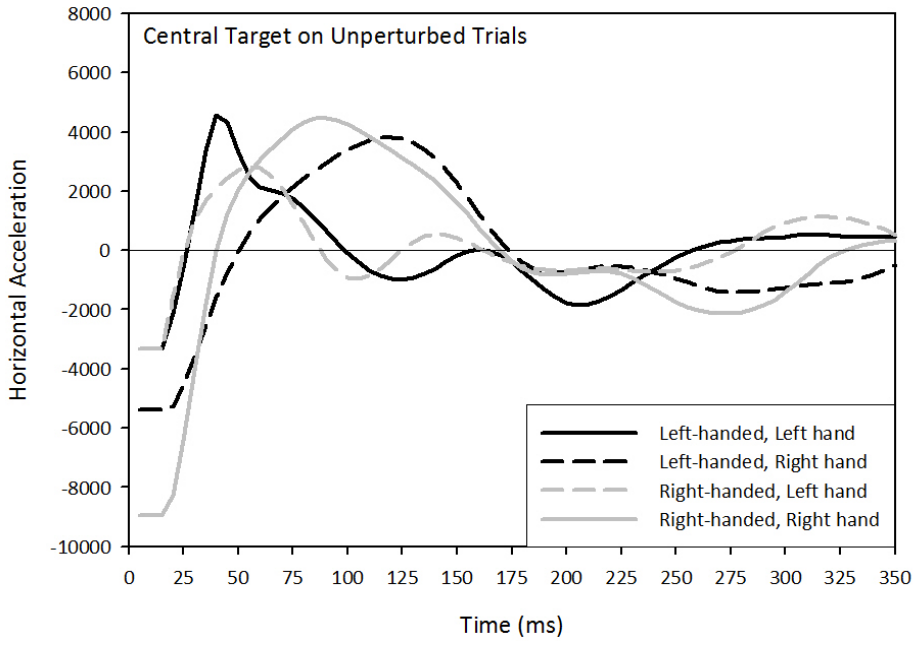
Horizontal Acceleration Profiles

A mixed model ANOVA analysing dominant hand (left, right) and acting hand (left, right) was run on the horizontal acceleration profiles produced in the unperturbed trials, when a stationary central target was presented. In order for any effect to be considered, any effect had to remain significant for 50ms (10 consecutive temporal bins).

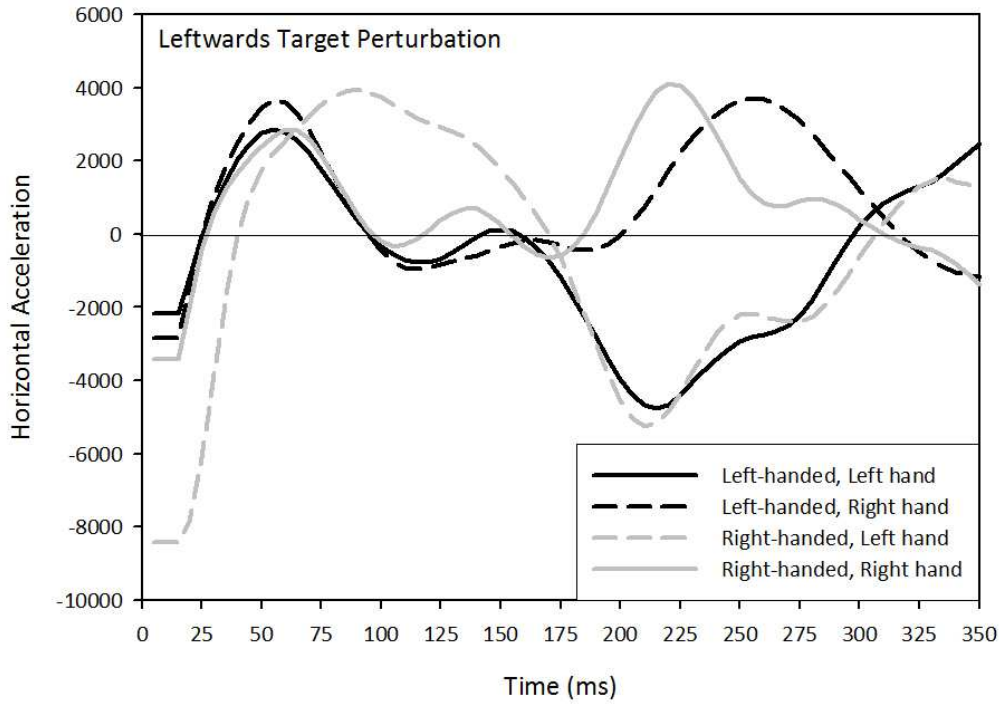
There was no statistically significant effect of the participant's dominant hand at any frame of the movement, although the hand used to perform the pointing task did have an effect. As can be seen in Figure 39, from 80ms into the movement until 150ms, there is a significant difference between the acting hands [$p \leq 0.031$], with the right hand producing more rightward acceleration when moving towards a central target. There is also a second reliable stage of the movement, between 250 – 350ms [$p \leq 0.025$], when the right hand moves leftwards, and the left hand moves rightwards, presumably to correct for the initial rightwards horizontal acceleration at the beginning of the movement.

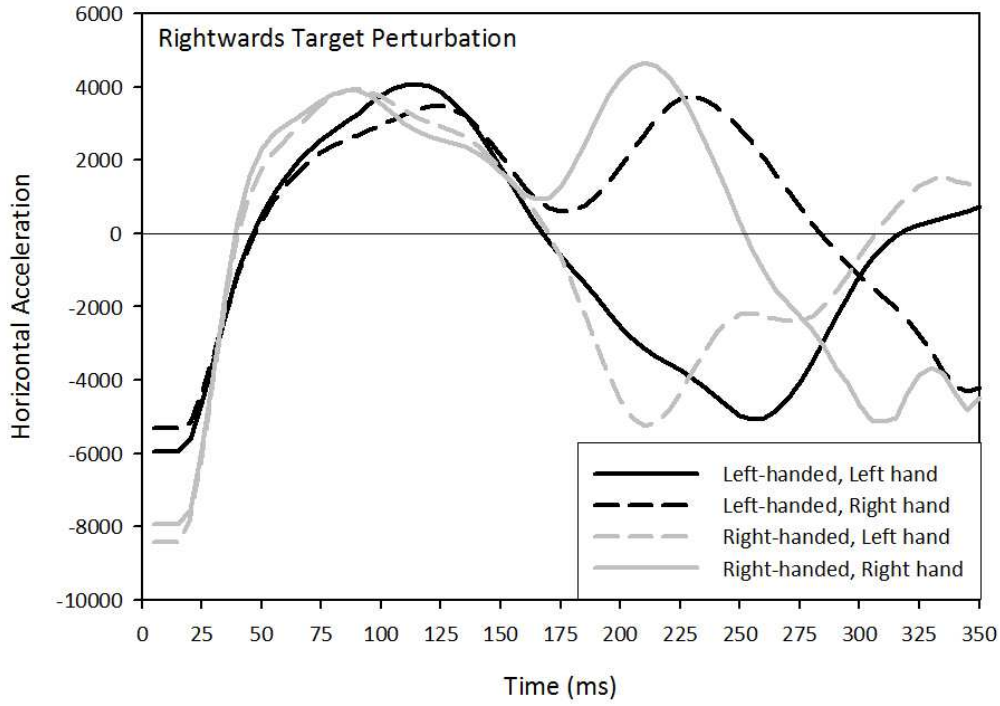
Figure 39: The mean horizontal acceleration profiles for movements towards centrally presented stationary targets. The Left-handed participants are plotted in black lines and the right-handed participants are plotted in grey lines. The dashed lines denote performance with the non-dominant hand.



A further mixed model ANOVA was performed on the perturbed trials with dominant hand (left, right) as the between subjects factor and acting hand (left, right) and perturbation direction (left, right) as the within subjects factors. Similarly to the unperturbed trials, there was no significant effect of hand dominance, as can be seen in Figure 40 and the hand used to perform the task became statistically significant at 85ms [$p \leq 0.025$]. There was also a main effect of perturbation direction from 180ms [$p \leq 0.021$], with leftwards perturbed targets resulting in a greater horizontal acceleration in the leftwards direction. The analysis also revealed a significant dominant hand x perturbation direction interaction at 245ms, with left-handed participants producing more lateral corrections in the later part of the movement, especially to the leftwards perturbed trials, potentially correcting for a less accurate tracking of the target perturbation.

Figure 40: The mean horizontal acceleration profiles for movements towards leftwards and rightwards perturbed targets. The Left-handed participants are plotted in black lines and the right-handed participants are plotted in grey lines. The dashed lines denote performance with the non-dominant hand.





Summary

As with the previous experiments presented within this thesis, a rightward advantage was observed in Experiment 9, yet the bias for increased correction efficiency extended beyond the ipsilateral advantage. Right-handed participants moved quicker and produced more corrections that were initiated earlier than the left-handed participants. Interesting though, this same pattern of results is true for all participants using their right hand, irrespective of handedness. The right hand produced shorter MT and DT and earlier CT, especially when moving towards a rightwards perturbed target, but this speed resulted in a cost in endpoint accuracy, as demonstrated in Figure 37, with more degrees of error in these same trials. All participants produced more corrections with their right hand than their left hand, and these corrections were initiated earlier, as revealed by the horizontal acceleration analysis.

Experiment 9: Discussion

The findings of the current experiment corroborate the findings of other experiments presented in this thesis. The rightwards bias which has been observed throughout the reported experiments is evident in the current experiment, and appears to extend from a rightwards perturbed target to performing with the right hand, to being right-hand dominant. Even in the unperturbed trials, when the target is presented in a central location on the screen, right-handed participants moved faster towards the target and were quicker to reach PV, with either hand in comparison to left-handed participants. All participants however, produced shorter MT and higher PV with their right hand independent of their preferred hand.

A similar pattern was observed in the perturbed trials, with right-handedness, using the right hand, and a rightwards jump direction all producing shorter MT in comparison to the left-sided counterparts. Furthermore, there were no statistical differences in the TPV, suggesting that the differences in MT occur after PV has been reached (Todor & Cisneros, 1985; Fisk & Goodale, 1985; Roy, Kalbfleisch & Elliott, 1994; Elliott et al., 1995; van Doorn, 2008). This was confirmed by the DT analysis and illustrated in Figure 36. This would allow the left hand to spend longer in the final deceleration phase of the movement, providing the opportunity for corrections to be made to the ongoing trajectory (Carlton, 1981b). However, the endpoint accuracy was poorer for movements made with the left hand, with a larger degree of error in comparison with movements made by the right hand, and this was evident in both left- and right-handed participants.

There was an interesting pattern however, with less complete corrections produced when pointing towards a rightward perturbed target with the right-hand than a leftwards perturbed target, which appears to go against the findings

in the literature. Fisk and Goodale (1985) and Roy et al. (1994) have shown that the right hand in rightwards hemispace as more accurate compared to a movement towards a leftwards target or when using the left hand, and so in the current experiment, although the corrections made by the right hand were more efficient, the final end point of the trajectory fell short of the final target position.

In terms of the corrections produced, there appears to be a biomechanical advantage to reaching towards targets that are perturbed into ipsilateral space, as illustrated by the CT and Individual corrections analyses, but overall, the right hand out-performs the left on each of the dependent variables. If the biomechanical explanation were to be fully supported, there would be an equal efficiency in the left hand for targets presented on the left, which is not evident in the current study. Furthermore, on variables such as MT and CT, right-handed participant's performance with their left hands, exceeds that of left-handed participants using their preferred left hand. Fisk and Goodale (1985) ruled out a biomechanical explanation for their findings as the eccentricity of the target presentation influenced the production of ipsilateral and contralateral movements in different ways. In the ipsilateral reaches, the maximum velocity was increased as the target eccentricity increased, resulting in movements of a similar duration, whereas the contralateral reaches compensated by increasing the movement times to prolong the deceleration phase of the movement. A similar pattern was evident in the current study, with longer MT and deceleration phases for contralateral targets. The DT analysis revealed that the right hand spent less time after PV in the deceleration phase, than the left hand did, especially for reaches towards ipsilateral targets. These results suggest that the right hand is specialised for this type of task, independent of handedness, although those who are right-hand dominant potentially have the opportunity to become more skilled through practice.

An additional component of the right hand advantage observed through out the experiments in this thesis could be a combination of attentional constraints and the specialisation of the left hemisphere. In terms of the speed of the movement, the timing of the correction, and the number of corrections produced, the rightwards direction of the target perturbation had a significant advantageous effect. This suggests that the left hemisphere may not only be specialised in the control of the complex motor output, but a target that jumps into the right visual field may also receive enhanced detection from the specialised hemisphere. This two-way hemispheric specialisation for detection and control could be additive to the effects observed of the advantage for the right hand when reaching for ipsilateral targets, beyond the functional biomechanical constraints.

Experiment 9 has established that the automatic pilot is more efficient when reaching towards a rightward perturbed target with the right hand, and that this advantage occurs independently of handedness. The predominance of the right-sided effect supports the conclusion that the left hemisphere is crucial in execution of accurate reaching and grasping, with specialisation for the organisation of the sequencing of complex motor movements (Goodale, 1990).

Further support comes from the neuropsychology literature, with studies of individuals who have damage to the substrates of the dorsal stream associated with the automatic pilot. In these individuals, aiming movements made with the right hand following damage to the left hemisphere are more severely impaired than movements made with the left hand following right hemisphere damage (Perenin & Vighetto, 1988). Furthermore, those with left hemisphere damage had difficulty controlling movements with their right hand anywhere in space, where as those patients who had suffered right hemisphere damage had difficulty with their left hand only in the contralesional hemifield (Perenin & Vighetto, 1988). The complexity of these deficits broadens the scope of questions to be asked about the automatic pilot and the role of the dorsal stream, within the context of manual asymmetries and hemispheric

specialisation. The complex relationship between motor performance, the automatic pilot and damage to the dorsal stream will be investigated and discussed in more detail below.

Experiments 10 and 11: Introduction

What is optic ataxia?

The processes responsible for the automatic pilot are situated in the posterior parietal cortex and require input from the dorsal pathway. As discussed in Chapter 1, it is understood that the dorsal stream processes the visual information required to guide action. This information is processed without conscious awareness, and is sensitive to target features such as luminance, movement and location (Milner & Goodale, 1995). Damage to this area can have consequences for the visuomotor abilities of the individual, and can result in difficulties in acting towards and locating objects without visual guidance.

Bálint (1909, as cited in Harvey & Milner, 1995) identified three symptoms as a result of bilateral parietal damage: optic ataxia, oculomotor apraxia and simultanagnosia, which became known collectively as Bálint's Syndrome. Patients with Bálint's Syndrome would have difficulty reaching for objects, difficulty initiating saccades and would have an inability to attend to more than one object at a time (Bálint, 1909; Harvey & Milner, 1995). Working as a neurologist during World War I, Holmes (1918) also noted that patients with bilateral parietal lobe lesions had impairments with visually guided movements. He described a patient who used his fingers in an attempt to see. The patient could see the object but was inaccurate in trying to reach for it and gab it. Holmes described the patient as searching the object out with his fingers,

coming into contact with a nearby object and feeling his way along to reach the desired object.

Although first reported in interaction with these other deficits, optic ataxia, or 'optische ataxie' can occur in isolation, and is the inability to accurately coordinate visually-guided movements. This inability occurs without motor, somatosensory, visual field or visual acuity deficits (Damasio & Benton, 1979; Perenin & Vighetto, 1988), and many patients are able to accurately reach towards proprioceptively, or auditory defined targets in the same locations that they misreach under visual guidance (Perenin & Vighetto, 1988).

Optic ataxia is most evident following bilateral damage, but can also result from unilateral lesions, and involve either one or both hands operating in either one or both visual fields (Damasio & Benton, 1979). The cases described by Bálint (1909) and Holmes (1918) were of bilateral patients who misreached across both visual fields, however more recent research has described unilateral patients with misreaching only in contralesional visual field (Castaigne et al., 1975, as cited in Jeannerod, 1986; Rondot, de Recondo & Ribadeaud Damas 1977; Levine, Kaufman & Mohr, 1978). It is now understood that optic ataxia can consist of hand and field effects, which allows for a number of combinations of possible reaching deficits. The term 'field effect' is used when both hands are affected when operating in the contralesional field, and the term 'hand effect' is used when the contralesional hand is affected in both visual fields (Perenin & Vighetto, 1988). There is also thought to be a relationship between the side of the lesion and the effects demonstrated, with right hemisphere damage resulting in a field effect and left hemisphere damage resulting in a hand and a field effect, suggesting hemispheric specialisation or asymmetry in the functional organisation of the PPC (Perenin & Vighetto, 1988). Although there can be a combination of hand and field deficits, there is a consistency in the literature of reporting accurate, or near to accurate, performance when reaching in central vision (Auerbach & Alexander, 1981; Perenin & Vighetto, 1988;

Jeannerod, 1986; Jakobson, Archibald, Carey, & Goodale, 1991; Milner et al, 1999; Rossetti & Pisella, 2002).

Impairments in optic ataxia

Bálint was able to identify that optic ataxia was not due to an impairment in spatial localisation or motor coordination, as his patient was able to point accurately with the unaffected hand and with the affected hand under visual guidance (Harvey & Milner, 1995). Perenin & Vighetto (1988) were able to further demonstrate that optic ataxia is a specific visuomotor disorder, independent of visual space misperception, which equally affects the proximal, reaching and transport phase of the movement and the distal phase, encompassing the shaping of the hand for grasping. Additional research has demonstrated that the grasp component of the movement is also impaired, as are visually guided movements such as anticipatory hand orientation (Perenin & Vighetto, 1998) and grip size (Jeannerod, 1986; Jakobson et al, 1991).

The main deficit to be investigated within the following series of experiments is the observed impairment in online motor control, which has been suggested by one research group as reflecting a specific deficit of the automatic pilot (Pisella et al. 2000). The Pisella et al. (2000) study has been described in detail earlier in Chapter 2, although this discussion mainly focused on the findings from the control participants. These participants were able to produce fast 'automatic' corrections in response to a target location perturbation, and were unable to override the compulsion to correct towards a new target location, even when instructed to stop their movement if they saw the target jump.

In addition to the healthy participants, Pisella et al. (2000) also carried out the same experiments with an optic ataxic patient called IG. Unlike the control participants, IG did not produce any corrective movements in the location-stop

condition, and the corrections she did produce in the location-go condition were slow and occurred late in the movement trajectory. When required to point to a target in a new location, defined by a colour switch, IG produced a normal range of slow corrective movements with her reactions to the colour change similar to those of controls. Pisella et al. (2000) concluded that IG was unable to produce the fast corrections observed in the healthy control participants, and that the ability to produce fast corrections was located in the PPC, the area of the brain where IG had sustained injury. IG was not drawn towards the new target location in the location-stop condition, and she was able to produce apparently normal performance when the jump was defined by a colour switch, due to her reliance on ventral stream processing. When the dorsal stream is damaged, the system compensates by using the ventral stream to complete the task, however, the ventral stream processes are slower and therefore it takes time for IG to respond to the target location perturbation.

The main conclusion from the Pisella et al. (2000) study was that the PPC was necessary for online motor control, especially for the production of automatic corrections, but not for movement planning or intentional motor control. By employing another double-step task, Gréa et al. (2002) were able to confirm this conclusion by requiring IG to correct her movements online to compensate for an inaccurate initial motor programme. The Gréa et al. (2002) set up involved the location perturbation of a physical object, which IG was required to grasp. Gréa et al. (2002) hypothesised that if IG was unable to correct her movements online, then she would be likely to close her grip around the location of the original target.

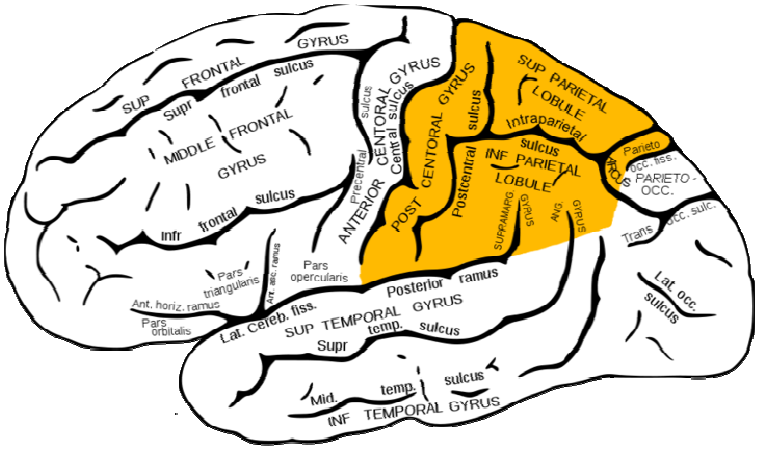
This is exactly what they found. IG was unable to correct towards the new location, and instead produced two movements, firstly to the original location and then towards the new location, as evidenced by two grip aperture peaks in 100% of perturbed trials. On the unperturbed trials however, IG performed similarly to controls, and produced an accurate grasp in 91% of trials. Her early

movement markers were similar to controls, but IG took longer in the deceleration phase of the movement, presumably to compensate for impaired fast feedback processes (Gréa et al., 2002). IG's sensorimotor planning was seemingly unimpaired, and she was able to plan and execute accurate grasping movements. What she was unable to do however, was update that initial motor programme to accommodate the target perturbation. For IG's aiming movement to accurately land on the new target location, she needed to complete the planned movement to the old location before planning and executing the second movement.

A Double Dissoication?

The sorts of deficits present in optic ataxia are thought to be due to damage to posterior parietal lobe, highlighted in yellow in Figure 40, especially Brodmann areas 5 and 7, including the superior parietal lobule (SPL) and the intraparietal sulcus (IPS) (Levine et al., 1978; Damasio & Benton, 1979; Auerbach & Alexander, 1981; Perenin & Vighetto, 1988), within the visual dorsal stream (Rossetti et al., 2003), where the automatic pilot is thought to be located. The evidence of the location of IG's brain lesion suggests the PPC as the structure which guides the hand to target during the course of the movement, with (IPL) implicated in movement planning (Glover, 2003; Gréa et al., 2002; Pisella et al., 2000; Rossetti, Pisella & Vighetto 2003). As discussed in Chapter 1, there is a second parallel visual pathway, the ventral stream, which runs from occipital to inferior temporal cortex, and processes rich information about colour, shape and texture (Milner & Goodale, 1995).

Figure 40: A diagram of the parietal lobe (adapted from Gray, 1918), showing the location of the superior parietal lobule (SPL) and the intraparietal sulcus (IPS), which are thought to be implicated in producing the patterns of behaviour seen in optic ataxia.



Optic ataxia results from damage to the occipitoparietal areas and thus damage to the dorsal stream, which means that reaching and grasping is impaired, but object recognition is unimpaired. In contrast, damage to the ventral stream can result in visual form agnosia, which creates impaired object recognition, but the person is able to reach and grasp the objects that they cannot describe. This functional double dissociation between optic ataxia and visual agnosia has been exploited in the literature as means to investigate the pathway for goal-directed action and the pathway for perception (Milner & Goodale, 1995; Rossetti et al., 2003).

As well as the anatomical distinction between the two processing streams, there is also a temporal difference in the speed the information is processed by each pathway (Rossetti et al., 2003). The magnocellular make up of the dorsal pathway allows for shorter processing latencies, and the parallel processing within the dorsal pathway means that information is processed faster than in the ventral stream. In optic ataxic individuals, the ventral stream is intact, and this may be how IG was able to perform similarly to controls in the colour-go condition in Pisella et al.'s (2000) study, as colour is an attribute processed by

the intact ventral pathway. Furthermore, the lack of the dorsal stream-driven fast corrections, meant that IG was also able to stop her movement in response to the location perturbation, and resulted in the late corrections towards the new location in the go condition. IG was therefore able to complete the task in the location-go condition, but slower because of the reliance on other slower brain processes. Therefore, by enforcing a delay between stimulus presentation and the response, and allowing the system to make use of the intact visual pathway, patients with optic ataxia should show increased performance on tasks they are impaired on with immediate responses.

This hypothesis was tested on an optic ataxic patient, MH, by Rice et al. (2008), who attempted to bring together information already established to test whether MH's performance would be improved following a delay before movement initiation. The Rice et al (2008) study consisted of three experiments. The first was used to establish MH's hand and field deficits on simple pointing task, the second established MH's obstacle avoidance abilities and the third experiment required MH to avoid obstacles after a delay.

Experiment one consisted of four possible target locations, two on the left and two on the right. The target positions were 5cm apart and 20cm from starting point, with one target presented at a time. A fixation point was located 60cm away from the starting point. MH was required to point to the target using his left and right hands, in fixation and non-fixation conditions, which were all separately blocked. MH's pointing performance was least accurate with his right hand, least accurate when pointing in peripheral vision (i.e. in the fixation condition), and worse for targets presented on the right than on the left. Additionally, MH was slower moving his right hand and movement times were slower in the fixation condition. This pattern of performance demonstrates MH's difficulties pointing with his right hand when acting in his right visual field.

In the second experiment, MH was required to point to a target that was presented between two obstacles. There were four possible obstacle locations, two on the left and two on the right, located 25cm from start position, and either 8cm or 12cm from the midline. The target was presented 20cm beyond the obstacle locations. Liquid crystal shutter glasses (Plato System, Translucent Technologies, Toronto Canada) were used to restrict the viewing time of the array, and closed upon movement commencement. There was no difference between MH and the controls in accuracy, when reaching with the left hand, but MH performed significantly worse when reaching with his right hand and when a right obstacle was present. Furthermore, MH had a longer reaction time for his left and right hand compared to controls. Rice et al. (2008) highlight the similarities in MH's performance across experiments one and two, with deficits when reaching with his right hand and when the target or obstacle is presented in his right visual field. These findings replicate those of Schindler, Rice, McIntosh, Rosetti, Vighetto and Milner (2004), who demonstrated that the two optic ataxic patients in their study, IG and AT, did not account for the location of the obstacle cylinder in the trajectories of their reaching responses.

The third experiment conducted by Rice et al. (2008) was the same as Experiment two, but with an added five second delay between the glasses closing and the beginning of the movement. With this modification, MH's pointing performance was no different from controls with his left *or his right hand*. Analysis demonstrated that there was less variability in the trajectories of the pointing movements than in Experiment two, demonstrating that MH's deficit in obstacle avoidance in right hand/right field reaching disappears when there is a delay before reaching.

These findings are discussed by Rice et al. (2008) as further support for the role of the dorsal stream in obstacle avoidance. As mentioned, Schindler et al. (2004) also revealed a failure to modify a reaching trajectory in the presence of an obstacle in two other optic ataxic individuals. Furthermore, Rice et al. (2006)

demonstrated that two patients with visual form agnosia, resulting from ventral stream damage, were able to complete the obstacle avoidance task as accurately as controls. The ventral stream does not appear to be implicated in the automatic avoidance of obstacles, as the individuals with visual form agnosia were able to use their intact dorsal stream to guide their movements between the obstacles to reach the target location. IG and AT were unable to do this, due to their impairment in dorsal stream functioning, as was the case with MH in Experiment Two. In Experiment Three however, the five second delay potentially forced participants to rely on a memorised representation of the workspace, derived from ventral stream processing, thus bypassing the damaged dorsal stream in the case of MH (Milner et al., 1999; Milner et al., 2001; Rice et al., 2008).

Rice et al. (2008) observed that MH's obstacle avoidance behaviour "shows a pattern of visuomotor impairment closely related to his accuracy in a visual pointing task" (Rice et al., 2008, p. 1556). MH failed to use extrafoveal visual information effectively for immediate movement guidance in both pointing to a stationary target and when required to avoid obstacles in order to reach a target. It could be questioned therefore whether MH's online correction behaviour follows the same pattern of his misreaching, in the same way as his obstacle avoidance behaviour does? Specifically, it seems possible that all of these behavioural impairments result from a core inability to use extrafoveal visual information to drive immediate action.

This question is explored in Experiments 10 and 11. If MH is impaired in acting towards stationary targets with his right hand and in his right visual field, it could be expected that his automatic corrections would also be impaired in the same way. Experiment 10 was the standard double step experiment, as described in Experiment 1, and was conducted in free vision with both MH's left and right hands. Experiment 11 was similar to Experiment 10, but also employed additional fixation crosses on the left and the right of the target

locations. Experiment 11 was conducted using controlled fixation and with MH's right hand only as in the Rice et al. (2008) study, MH displayed intact obstacle avoidance in all three other hand/field combinations. This second experiment would allow the investigation of MH's pointing accuracy at two different eccentricities within the left and right hemifields, and potentially disentangle the importance of hemifield or jump direction as an influence over the pattern of impaired corrections.

It was hypothesised that in Experiment 10, MH would show impaired corrections for rightwards target jumps when responding with the right hand, but would produce normal (or near-normal) patterns of corrections under all other conditions. Thus, we predicted that MH's pattern of online correction would mirror his pattern of misreaching. In Experiment 11, it was predicted that MH would be impaired in his corrections for all target jumps in the Fixate Left condition, as both targets would be presented in his ataxic right hemifield, and would perform accurately in Fixate Right condition. It is hypothesised that T2 location, and therefore the hemifield would be the influential factor in MH's correcting impairment, rather than jump direction.

Experiments 10 and 11: Methods

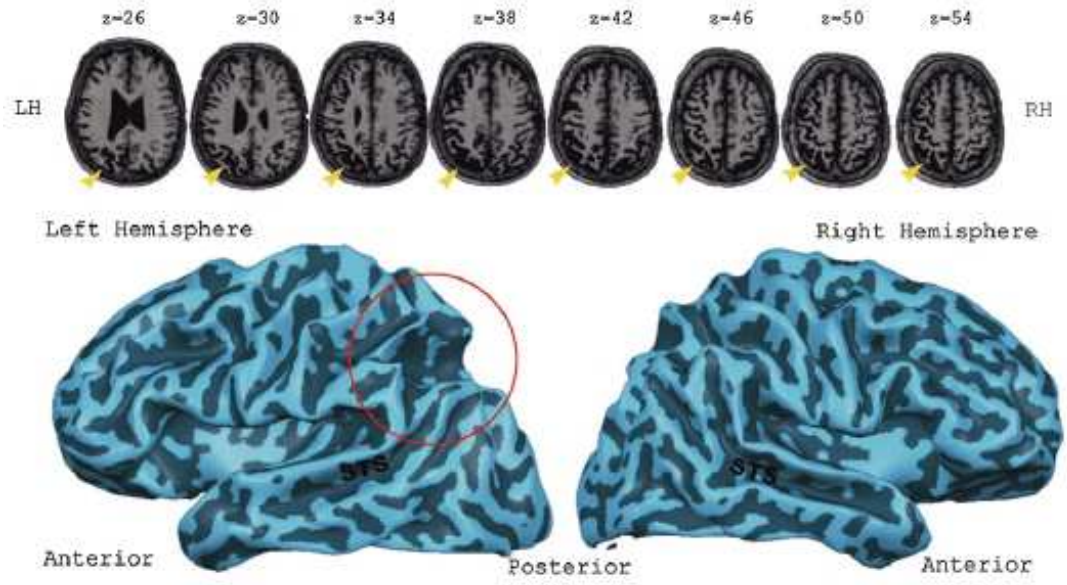
Participant

MH suffered carbon monoxide poisoning at the age of 42 years, and was aged 52 years old at the time of testing. His anoxic brain injury resulted in right sided weakness and raised sensory thresholds on the right. Upon hospital admission, MH was able to walk and use both his hands, but had difficulty with activities of daily living (ADLs), such as dressing, using a knife and fork and writing. An MRI

scan (performed in 2006; Figure 41) confirmed the findings of the original CT scan and reported lesions to the left parietal region, including the occipital-parietal borders, the intraparietal sulcus, and the superior parietal lobe and also changes in the right posterior parietal cortex. There were bilateral lesions of the lentiform nucleus and the heads of the caudate nuclei, and damage to a lesser extent to the left frontal (premotor) region.

MH, as a clinical case study, has been well described in previous literature, including Riddoch et al. (2004), Kitadono and Humphreys (2007), and Rice et al. (2008).

Figure 41. MRI scan of M.H.'s lesion. Axial slices taken from the 3D anatomical MRI scan of patient M.H. (*z*=24 to *z* = 54) showing the site of the lesion in the left parietal lobe with arrows (top panel). The cortical surface of M.H. was rendered in 3D using *Brain Voyager* QX 1.7 software (Brain Innovation, Maastricht, Netherlands) to produce inflated surfaces of the left and right hemispheres that exclude the lesioned brain matter. The site of the lesion is marked with a circle on the left inflated surface. Figure used with permission from Rice et al. (2008).



Design

Experiment 10 was made of four blocks of 90 trials, with 10 practice trials presented before the start of each block. Before the first block, MH was given 20

unperturbed practice trials and then 20 perturbed practice trials in order to get used to the task and the required speed of response. Each block was made up of 60 unperturbed trials and 30 perturbed trials, with the target perturbation to the left and the right on an equal number of trials. Two blocks were completed with the left hand and two with the right hand, in an A-B-A-B design, starting with the dominant hand, and all blocks were completed in free vision.

Experiment 11 was made up of four blocks of 92 trials, with a 30% perturbation rate. Twenty practice trials were presented before the first block and 10 practice trials presented before the start of the proceeding three blocks. The target locations were identical to those used in Experiment 10, with the addition of two potential fixation locations. A fixation cross was presented on each trial 60mm from the centre of the screen in either a left or a right location, and MH was required to fixate the cross throughout the trial. The side of presentation for the fixation cross was intermixed within each block and is determined pseudo-randomly. MH performed with his right hand only.

Apparatus

Stimuli were presented on a 17" monitor (resolution 1024 x 768 pixels) in front of MH, with a distance of 505mm from centre of screen to the start button, in a dimly illuminated room. The stimulus was a white dot, 10mm in diameter, presented on a black background to reduce glare. On all trials, the target appeared 27mm to the left or 27mm to the right of the centre of the screen when the button was pressed, and either stayed in its initial position (unperturbed trials) or made a jump to 27 mm to the left or right of the central position in the perturbation trials.

MH's hand movements were tracked using a 3D motion tracking system (ProReflex, Qualisys Ltd., Sweden) at 200Hz. A reflective marker was attached to the nail of MH's index finger.

Two tones were used to pace MH's movements. The first tone was sounded 350ms after movement commencement and MH was instructed to touch the dot on the screen in time with the beep. The second tone was sounded 1000ms after the start of the movement and MH was instructed to return to the start button after the second beep.

The apparatus used in Experiment 11 is identical with the addition of a grey fixation cross (15 x 15 pixels) presented either 60mm to the left or the right of the centre of the screen. To ensure fixation was maintained, a video camera was used to record MH's eye movements, which were monitored online during the task.

Procedure

The procedure for Experiments 10 and 11 was the same as reported for the GO condition in Experiment 1, with the exception of an additional instruction in Experiment 11 to maintain fixation on the cross throughout the trial.

Experiments 10: Results

Nine trials were removed from the analysis of the data from Experiment 10, as they fell outside the cut off of 3 standard deviations from the mean. The remaining data were used to perform separate Factorial ANOVAs for RT, MT, PV, TPV and AE to test the effects of hand (Left, Right), perturbation (unperturbed, perturbed) and side of Target 1 (left, right).

There was a significant effect of hand for all of the dependant variables. For the RT measure, MH's right hand was quicker than his left [$F(1,337) = 28.03$;

p<0.001] and in the analysis of AE, MH's left hand made more leftward errors [F(1,337) = 10.75; p≤0.001] in comparison with his performance using his right hand. In the other kinematic features of the pointing movements, MH's right hand performed significantly worse than his left hand in the free vision pointing task. His right hand had a slower movement time [F(1,337) = 86.24; p<0.001], a lower peak velocity [F(1,337) = 356.39; p<0.001] and took longer to reach peak velocity [F(1,337) = 83.72; p<0.001], than his left hand, as can be seen in Table 25 which lists the kinematic data from Experiment 10.

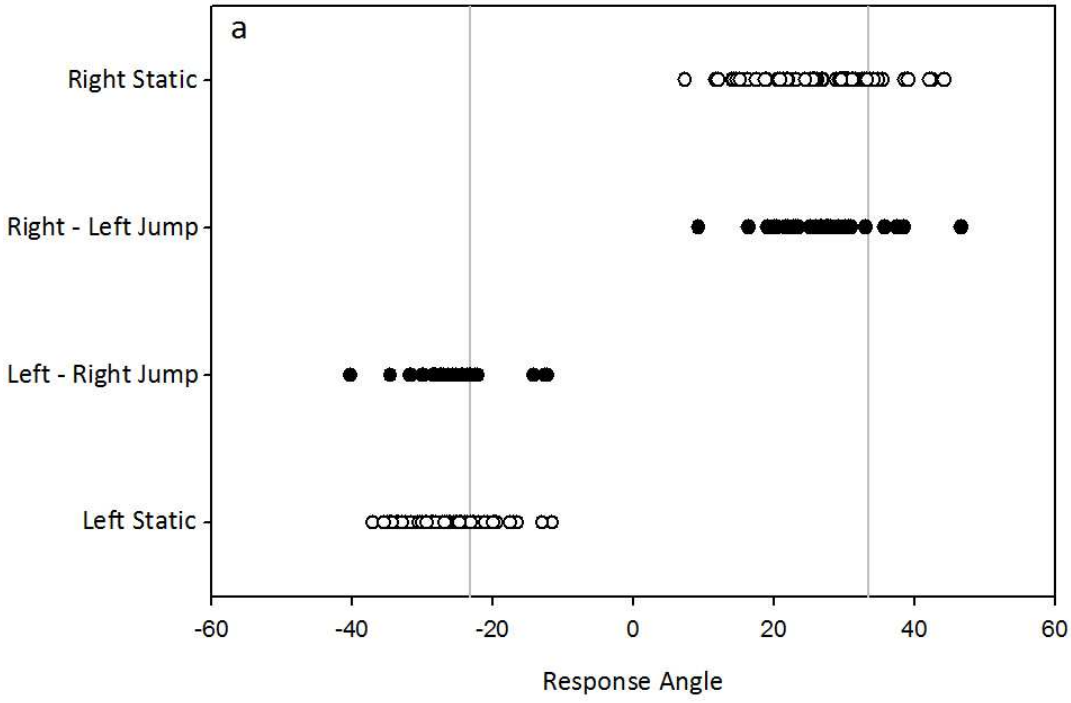
Hand used	T1 location	Perturb	RT	MT	PV	TPV	AE
Left Hand	Left	Static	373.8 (69.2)	342.3 (32.0)	2417.0 (201.9)	106.0 (24.7)	-0.5 (0.66)
		Jump	360.0 (78.9)	352.7 (39.1)	2327.9 (205.3)	122.7 (29.8)	-6.8 (0.5)
	Right	Static	384.0 (85.2)	367.2 (34.0)	2171.8 (178.0)	107.2 (27.1)	-0.8 (.08)
		Jump	394.1 (76.2)	364.8 (33.6)	2178.8 (164.6)	107.8 (23.2)	5.6 (0.9)
Right Hand	Left	Static	348.8 (43.9)	410.4 (50.2)	1841.5 (143.6)	139.8 (37.7)	-0.4 (.07)
		Jump	338.9 (33.4)	410.6 (34.4)	1828.8 (141.7)	147.7 (19.6)	-6.3 (0.6)
	Right	Static	335.2 (37.9)	385.0 (47.6)	1944.8 (194.6)	147.3 (40.4)	-0.3 (0.9)
		Jump	339.1 (34.8)	392.7 (38.4)	1942.1 (153.6)	142.0 (35.5)	5.6 (0.8)

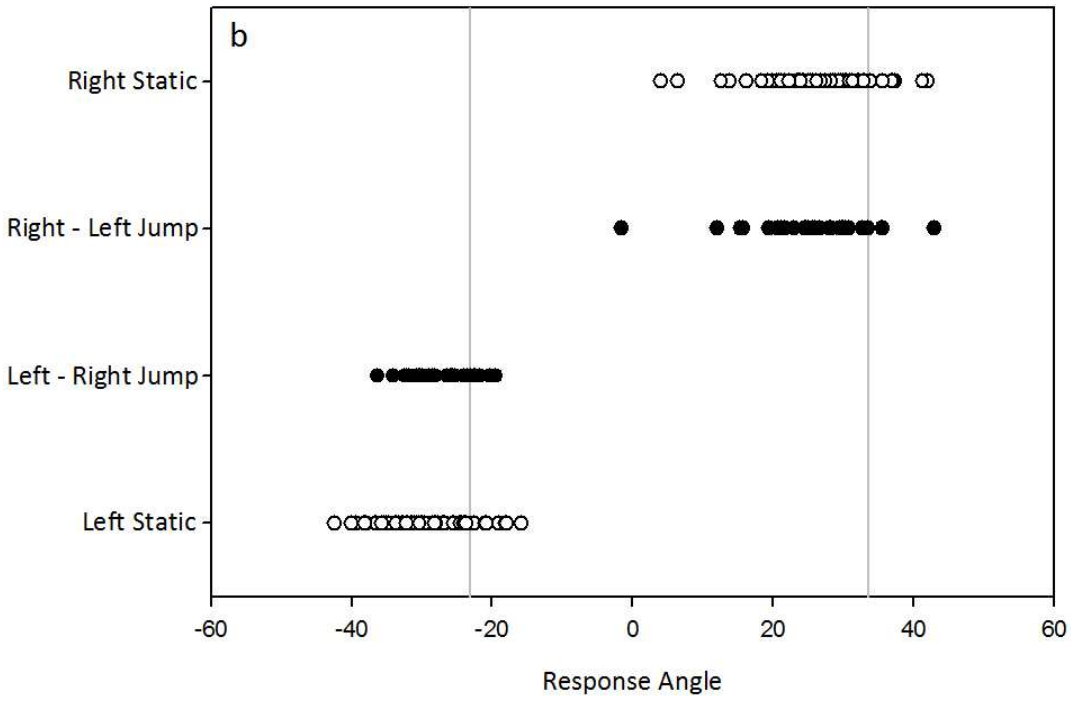
Table 25: The mean kinematic data from Experiment 10 – 3SD outliers removed

There was also a significant effect of the side of T1 presentation, with movements towards targets on the left reaching higher peak velocities [F(1,337) = 4.76; p<0.05], and larger leftward (hypometric) errors for targets on the left [F(1,337) = 4774.84; p<0.001]. In addition, there were also significant hand x side of T1 interactions. The movements made by MH with his left hand had a quicker reaction time [F(1,337) = 4.18; p<0.05], quicker movement times [F(1,337) = 18.88; p<0.001] and higher peak velocities [F(1,337) = 56.21; p<0.001] to targets presented on the left, as opposed to the right, and

movements made by MH using his right hand showed the opposite pattern, with quicker reaction times, quicker movement times and higher peak velocities to targets presented on the right, as opposed to the left. This is evidence of the biomechanical artefacts of the task, with movements towards the left being easier to complete with the left hand and vice versa (Fisk & Goodale, 1985), yet MH's right-handed performance is significantly worse overall than the movements made using his left hand.

Figures 42a and b: The endpoints of MH's (a.) left hand and (b.) right hand pointing performance on the unperturbed (white circles) and perturbed (black circles) trials in the free vision condition. The grey lines demonstrate the two target locations.





Figures 42a and 42b show the endpoints of MH's pointing movements, with his left hand and right hand respectively. As is evident from the figures, MH did not make any fast automatic corrections towards the new target location on the perturbed trials, pointing to the initial location of the target on every trial. This pattern of results occurred even though MH was free to direct his vision at the target, and also occurred when MH was using his left hand. These findings go against our hypothesis, which stated that MH would have difficulty correcting a movement towards a rightwards jumping target when pointing with his right hand. It is evident that MH has difficulty updating his movements with either hand and towards a target presented in either hemifield.

Experiment 11: Results

Six trials were removed from the analysis of the data from Experiment 11, as they fell outside the cut off of 3 standard deviations from the mean. The remaining data were used to perform separate Factorial ANOVAs for RT, MT, PV, TPV and AE to test the effects of fixation (Left, Right), perturbation (unperturbed, perturbed) and side of Target 1 (left, right).

For AE, there was a main effect of fixation, with larger errors produced when MH was fixating to the left [$F(1,349) = 14.92$; $p<0.001$]. This would be expected, as all targets would have been presented in his right ataxic hemifield. MH also produced larger errors towards the right target [$F(1,349) = 40.52$; $p<0.001$], in comparison with the target presented on the left. Notably, there was also a significant fixation x side interaction, with larger errors produced when attempting to point to the most peripherally presented target [$F(1,349) = 8.50$; $p<0.005$], especially when fixating to the left, and so reaching in the right hemifield to the right-sided target. Again, this would be expected, as these targets are presented the furthest from fixation. In Figure 43, the absolute error is plotted unsigned for MH's pointing performance in the baseline trials in Experiments 10 and 11. MH had difficulty pointing accurately to the target in Experiment 10, in the free vision condition, and as Figure 43 clearly shows, this difficulty is exacerbated by requiring MH to maintain fixation and perform the task in his peripheral vision. Figure 43 shows that MH makes very large errors when pointing to a target presented on the right, yet the figure also demonstrates that MH's pointing to targets on the left is also much worse than when in the free vision condition.

Figure 43: The absolute error of MH's pointing performance on the unperturbed trials in Experiments 10 (Free Vision, right and left hand) and 11 (Fixate Left and Fixate Right trials).

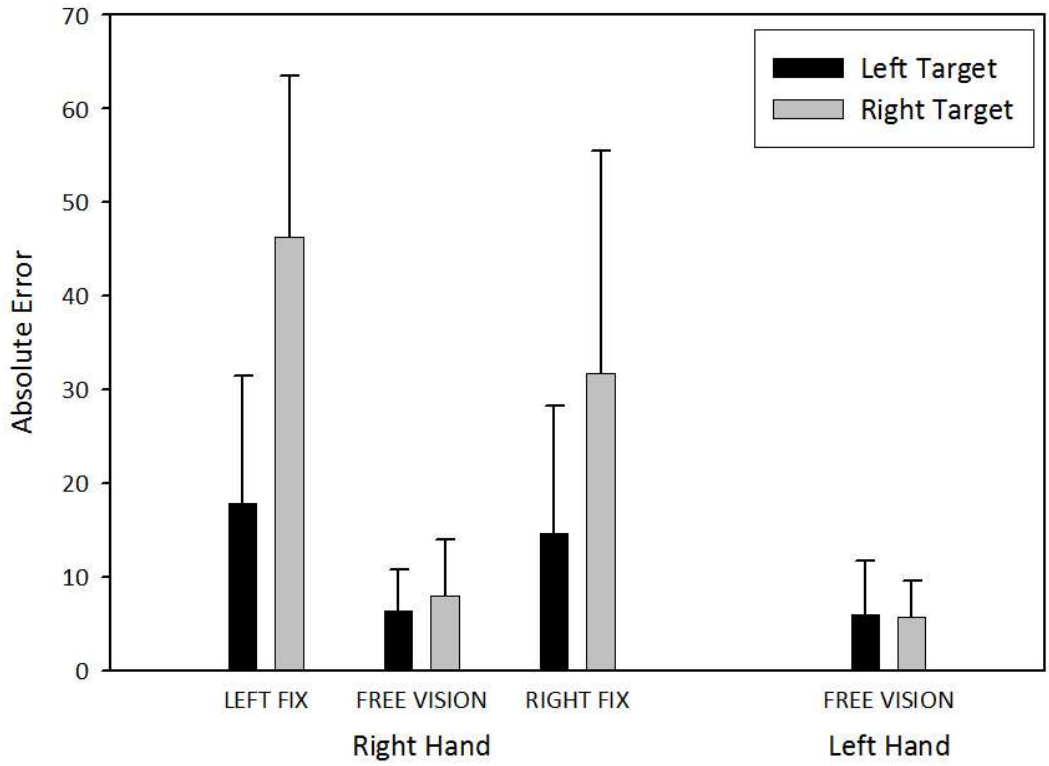


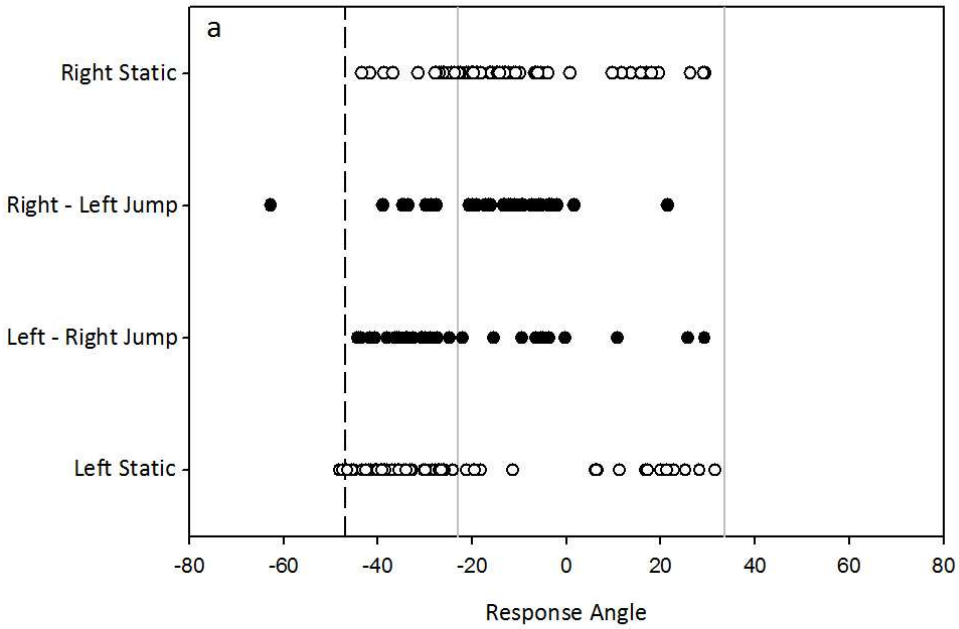
Table 26 contains the mean kinematic data for Experiment 11. There was no reliable effect of fixation, perturbation or side of target 1 presentation on MH's reaction times or the time taken to reach peak velocity. There was however, a statistically reliable effect of perturbation on movement time and peak velocity, with MH moving slower in the perturbed trials [$F(1,349) = 5.50$; $p<0.05$] and not reaching as high a peak velocity [$F(1,349) = 3.75$; $p\leq0.054$], as in the unperturbed trials. MH also produced movements with lower peak velocites towards targets on the left, and for both movement time [$F(1,349) = 10.45$; $p\leq0.001$], and peak velocity [$F(1,349) = 4.85$; $p<0.05$], there are significant three-way fixation x perturbation x side interactions, with movements towards a jumping target which started in the most peripheral location taking longer to complete and moving at a slower speed.

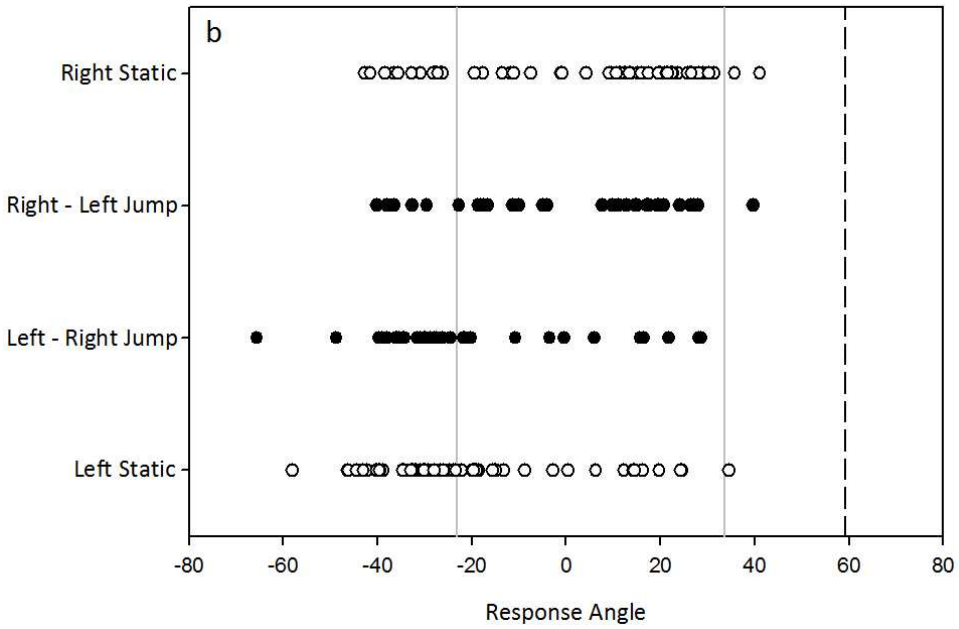
Fixation	T1 location	Perturb	RT	MT	PV	TPV	AE
Left Fixation	Left	Static	393.7 (68.0)	542.5 (57.7)	1425.1 (156.3)	205.8 (46.5)	0.0 (2.5)
		Jump	383.7 (68.0)	528.4 (49.7)	1433.2 (119.0)	194.8 (45.3)	-6.3 (2.3)
	Right	Static	401.2 (72.7)	516.4 (55.9)	1482.1 (137.1)	195.6 (43.7)	-5.2 (1.9)
		Jump	391.4 (62.4)	548.4 (54.1)	1445.9 (161.6)	202.1 (49.5)	0.8 (1.7)
Right Fixation	Left	Static	397.4 (66.0)	512.6 (40.80)	1471.0 (145.8)	212.0 (42.8)	.3 (2.2)
		Jump	385.1 (54.4)	547.4 (50.3)	1370.1 (130.9)	207.3 (38.0)	-6.0 (2.6)
	Right	Static	384.8 (70.3)	516.5 (52.8)	1482.8 (154.2)	202.4 (39.0)	-3.6 (2.7)
		Jump	384.6 (62.9)	520.0 (67.5)	1483.5 (168.6)	193.4 (41.2)	2.7 (2.6)

Table 26: The mean kinematic data from Experiment 11 – 3SD outliers removed

As in Experiment 10, MH does not make any fast automatic corrections in Experiment 11. This is not surprising considering the previous result, as it would be expected that MH would be able to correct his movements to a target perturbation in free vision, at least with his left hand to a leftwards jumping target, yet he was unable to. In terms of the descriptions of MH's pointing abilities published in the literature (Rice et al., 2008), we would expect MH to be able to correct towards targets in his non-ataxic left hemifield, as would be demonstrated in the trials with the right fixation cross. This was not the case as Figures 44a and 44b demonstrate.

Figures 44a and b: The endpoints of MH's pointing performance on the unperturbed (white circles) and perturbed (black circles) trials in the (a.) left fixation and the (b.) right fixation conditions. The grey lines demonstrate the two target locations, and the dashed black line demonstrates the location of the fixation cross.



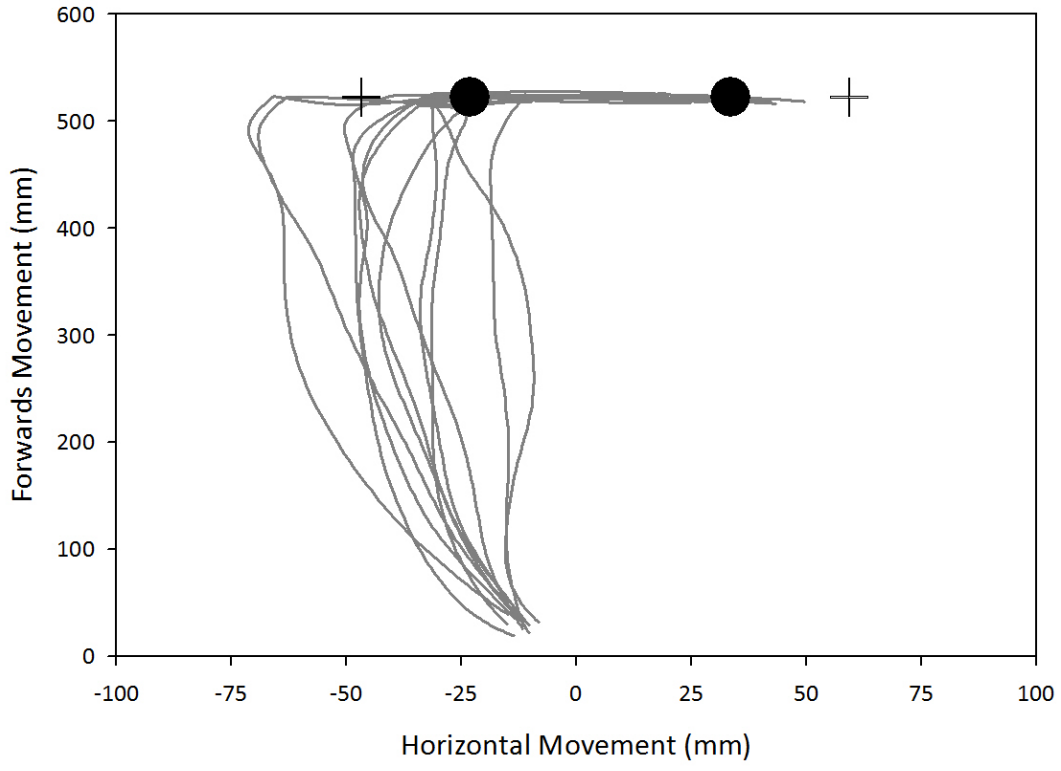


In Figure 44a, many of MH's pointing movements appear to be drawn towards the point of fixation, regardless of the location of the target on the screen. In

both the left and right fixation conditions, there is much more variability in MH's pointing responses, with the constraint of maintaining fixation causing problems with accurate pointing. The spread of endpoint responses has implications for the classification of the perturbed trials as corrected or uncorrected, however MH's performance in Experiment 10 suggests fast corrections towards the new target location are unlikely.

Figure 45 confirms the pattern of responses suggested in Figure 44a. Figure 45 is a plot of multiple trajectories from Experiment 11, in the left fixation condition for left-to-right perturbed trials. As can be seen, MH does indeed initially move towards the left fixation cross on some trials, and on most trials points to the location of the left target and then slides his finger across the screen to touch the right target.

Figure 45: A bird's eye view of a selection of trajectories of MH's pointing movements in the left fixation condition for left-to-right perturbed trials. The crosses indicate the locations of the fixation crosses (only one was presented per trial) and the black circles indicate the two possible locations of the target (not drawn to scale). In these trials, the leftwards target was presented first and would have been offset simultaneously with the onset of the target in the rightwards location.



Summary

In summary, MH was not able to successfully complete these tasks. He did not produce any fast corrections towards a target location perturbation, and in fact had difficulty pointing accurately to a stationary target in free vision with both his left and right hands. Although MH's performance was impaired with both hands in the free vision experiment, the data reveal that his right hand was slower in terms of the overall movement time, the peak velocity reached and the time taken to reach peak velocity, in comparison with his left hand. By moving slower, MH was able to be more accurate, producing smaller errors than when using his left hand. The side of T1 presentation in itself did not reliably affect the RT, MT, PV or TPV, except through the hand x side interactions, which potentially confirm biomechanical advantages for movements towards ipsilateral targets. However, it was expected that T1 location, in relation to MH's ataxic field, would have more of an effect on the kinematic features of the movement and endpoint accuracy. In Experiment 10, there were larger errors for targets presented on the left, irrespective of the hand used for the task, which goes against our hypothesis, yet in Experiment 11, the larger errors are evident in pointing movements towards rightward located targets, irrespective of whether they were nearer to or further from the fixation location.

Experiments 10 and 11: Discussion

Experiment 10 set out to characterise MH's ability to correct his aiming movements in response to a target location perturbation. It was predicted, that given the damage to his left posterior parietal region and previous published studies of MH, that MH would show impaired corrections for rightwards target jumps when responding with the right hand, but would produce normal (or near-normal) patterns of corrections under all other conditions. It was

predicted therefore, that MH's pattern of online correction would mirror his pattern of misreaching. The data do not support this prediction.

On the whole, the aiming movements made by MH with his right hand were slower, with slower movement times, lower peak velocities and longer times to reach peak velocity, which was as predicted, yet the movements made with MH's left hand produced greater endpoint errors. A study by Rice et al. (2008) established that MH's performance was poorer with his right hand and when pointing to a right-sided target. Experiment 10 confirms MH's poorer performance with his right hand, but inconsistent with the Rice et al. (2008) description, the current experiment also showed that MH benefited from pointing to ipsilateral targets, thus suggesting MH's performance was better when pointing with his right hand to a right target, as opposed to a target presented on the left.

The main finding from Experiment 10 is the startling demonstration that MH is unable to produce fast online corrections to a target perturbation with either hand, to a target in either hemifield. Figures 42a and 42b demonstrate that MH's pointing to a static target is variable and not especially accurate, but the endpoints of the movements towards a perturbed target appear to be very similar, with MH pointing to the original location of the target.

The lack of corrections in Experiment 10 was replicated in Experiment 11. It was predicted that MH's correction ability would be impaired for jumps in both directions in the Fixate Left trials, as the target would be presented in his ataxic right hemifield, but that MH would produce normal, or near to normal performance in the Fixate Right trials. It was predicted that T2 location would be the determining factor in MH's ability to update his movements online, rather than the direction of the target perturbation. These predictions were made however, when Experiments 10 and 11 were designed, and Experiment 11 was

conducted on the same day as Experiment 10, before the data from the earlier experiment had been analysed.

In support of the hypothesis, MH made more errors in the Fixate Left trials than the Fixate right trials, because when fixating the left fixation cross, both targets were presented in his ataxic hemifield. Additionally, MH made more errors when pointing to the right target, irrespective of the fixation condition, and especially made more errors when pointing with his right hand in his right visual field to the right-sided target, replicating Rice et al's (2008) finding. However, in complete contradiction to the hypothesis, Figure 43 demonstrates how much MH's endpoint accuracy was affected by being required to perform the task in the periphery of either visual field. As already discussed, MH's pointing ability to a static target was not particularly accurate in the free vision experiment, yet the magnitude of error dramatically increases when MH is required to fixate to the left or the right of the location of the target. Figures 44a and 44b plot the endpoints of MH's pointing movements and further confirm his inability to perform the task.

The interesting result, which is apparent in Figures 43, 44a, and 44b, is that MH is also impaired in his left hemifield. There are still high amounts of error in his pointing movements performed in the Fixate Right trials, during which the targets would have been presented in his left, non-ataxic, hemifield. Having to control movements out with foveal vision, in either peripheral field, is incredibly difficult for MH, as demonstrated in Figures 44a and 44b. In the Fixate Left trials (Figure 44a), MH's right hand appears to be drawn to the location of fixation, with many of the movement endpoints closer to the fixation cross location than is evident in the Fixate Right trials (Figure 44b). This can be interpreted as classic optic ataxic behaviour, with the hand movement being directed towards the direction of gaze (Ratcliff & Davies-Jones, 1972; Carey, Coleman, Della Sala, 1997; Buxbaum & Coslett, 1997), and is also observable in

the example trajectories from the left-to-right target perturbation trials, plotted in Figure 45.

The large errors and the variability in performance produced by MH in the unperturbed trials of Experiment 11 makes it difficult to interpret MH's performance in the perturbation trials. As can be seen in Figures 44a and 44b, MH does end some of his movements in the area of the T2 location, but due to the variability in the unperturbed performance, these trials are not classed as corrections. On reflection though, it does not appear that MH's correction ability is misrepresented in Experiment 11, as it would not be expected that MH's performance would improve with peripheral fixation, in comparison with performance in Experiment 10, but that the variability in MH's pointing is consistently high throughout the unperturbed and perturbed trials.

The lack of corrections in Experiment 11 does not allow us to disentangle the influence of hemifield over the influence of jump direction. Despite the lack of corrections, it can be tentatively concluded that MH's correction deficit is related to his misreaching. Our task may have been too difficult for MH to complete, as we observed difficulties in pointing to stationary targets presented in his left extrafoveal vision, and so, asking MH to deal with jumping targets may have been a step too far. One conclusion that can be drawn from the data of Experiment 11 is that the task is a very sensitive measure of optic ataxia. Our task may have revealed signs of asymmetrical bilateral optic ataxia in MH: MH did not produce any corrections with either hand, or in either side of space, he showed left-sided misreaching in Experiment 11, and does indeed have bilateral brain lesions.

The design of the current experiments was conceived to allow us to compare MH's reaching and correction ability in his ataxic and non-ataxic regions of space. If MH were a bilateral optic ataxic, then the only region of space that would not be affected would be central vision. Therefore, to address the

questions that still remain, it would be necessary to perturb the target to the unimpaired region of the visual field, to the point of fixation. This experimental design is employed in the next set of experiments.

Experiment 12: Introduction

As with MH, IG's pointing performance has also been well documented, and as with the hypothesis of Experiments 10 and 11, it would be expected that IG's online correction deficit would mirror her misreaching and her obstacle avoidance behaviour. Like MH, IG also failed to make adjustments to her reaching trajectory when there were obstacles present (Schindler et al., 2004), but could take account of the obstacles in a perceptual bisection task, performing similarly to controls.

The reaching movements in the Schindler et al. (2004) study were performed without visual feedback during the reach, and so the avoidance manoeuvres evident in the controls must have been pre-programmed rather then reactive. The authors concluded that the avoidance manoeuvres evident in the controls were built into the trajectory by dorsal stream processes, as neither IG, nor AT, another optic ataxic participant, were able to demonstrate this ability. Furthermore, these avoidance manoeuvres occurred without explicit instruction, suggesting they are executed automatically (Schindler et al., 2004). These same avoidance trajectories even occur in participants with unilateral visual neglect, with obstacles on the neglected side that are not well attended in explicit tasks, but are avoided in a manner similar to controls during reaching (McIntosh et al. 2004). Moreover, perceptual deficits caused by extensive damage outside the dorsal stream, do not seemingly interfere with this ability either (Rice et al., 2006). This cumulative evidence suggests the role of the

dorsal stream in the avoidance of obstacles and suggests automaticity analogous to online corrections.

IG's online correction ability has been discussed earlier in the chapter, with Pisella et al. (2000) and Gréa et al. (2002) demonstrating that she is unable to make short latency corrections to her ongoing reaching movements towards a displaced target. The control participants were able to touch the target in the new location during reaches that lasted only 200ms, but IG could only land on the new target location when her MTs exceeded 300ms, but was able to perform similarly to controls when the instruction was to abort the movement as soon as the target jump was detected (~300ms). Movements shorter than 300ms were not stopped, and the control participants found their hand in the new target location, where as IG would end her movement in the original location. These data imply that fast corrections are automatic and pre-conscious, implemented before any voluntary response can be made (Castiello et al, 1991; Goodale et al, 1986), and that these automatic responses are absent in IG. However, the fact that IG made an intentional stop response with normal latency suggests that she was not impaired in her conscious perceptual detection of the target jump, similar to her bisection performance in the Schindler et al. (2004) study. Pisella et al (2000) proposed that a specific visuomotor sub-function of the posterior parietal lobe is as an 'automatic pilot for the hand', adjusting reaching movements online, and that this function is impaired in optic ataxia (see also Gréa et al, 2002).

Himmelbach, Karnath, Perenin, Franz, and Stockmeier (2006) added an interesting dimension to the characterization of IG's online correction abilities, by showing that she can update her grip aperture to changes in object size, with a rapidity equivalent to that of healthy controls. They tested grasping of virtual objects in central vision, and IG's performance was taken as evidence against any general impairment of online correction. Instead, Himmelbach et al. suggested that the correction deficit, like optic ataxic misreaching, may chiefly

affect reactions to extrafoveal targets. This inference was based on the contrast between preserved grip updating in central vision and prior demonstrations of impaired updating of reaches to targets jumping away from central vision (Gréa et al, 2002; Pisella et al, 2000). More recently, a unilateral optic ataxic patient (CF, see Experiment 13) with combined left hand and left field misreaching was reported to show impaired online reach correction with the same combination of hand and field effects (Blangero et al, 2008). This correspondence supports a close association of impaired online correction with optic ataxic misreaching, implying that impaired online correction should be principally an extrafoveal problem. According to this idea, the online correction deficit could be just one specific manifestation of a more general inability to use extrafoveal visual information to guide immediate action.

However, the idea that impaired online correction should chiefly affect extrafoveal reaches is less than straightforward, since one must consider the location to which the reach is initially aimed as well as that to which it must be diverted. Using double-step tasks, previous studies have presented the target initially in central vision, displacing it to extrafoveal locations (Blangero et al, 2008; Gréa et al, 2002; Pisella et al, 2000). The impairments found establish that these patients, who typically reach accurately to fixated targets, have difficulty correcting towards ataxic fields. The jumped target location is thus important, but it is unclear whether the initial target location also matters, since this has never been varied. The simplest hypothesis would be that the online correction deficit in optic ataxia depends exclusively upon the location towards which the correction must be made. This simple hypothesis predicts impaired updating if the target of an ongoing reach jumps to a part of the visual field affected by optic ataxia, but rapid updating if it jumps to a non-ataxic location.

The first purpose of Experiment 12 is to test this hypothesis in patient IG. If her online correction deficit is determined solely by the location towards which the correction is required, then IG should be slow to correct if a target jumps from a

foveal to an extrafoveal location, but greatly improved if it jumps from an extrafoveal location to her point of fixation.

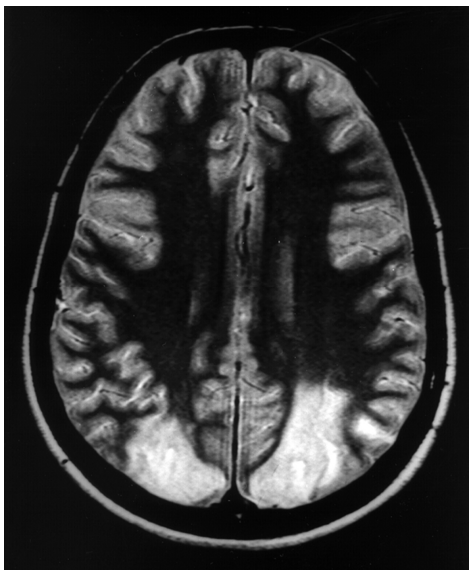
Secondly, this study seeks to clarify the relationship between IG's online correction deficit and her perceptual awareness of the target jump. Pisella et al (2000) found that IG was as fast as healthy controls in reacting to a target jump by voluntarily stopping her movement, which was taken to mean that her perception of the jump was unimpaired. Unlike online correction, however, a stop response does not require the direction of the jump to be discriminated, so it is possible that IG could have solved the task just by monitoring central vision for the disappearance of the original target. To more fully assess any perceptual contribution to IG's online control deficit, we included a perceptual choice reaction time task, requiring speeded discrimination of jump direction.

Experiment 12: Methods

Participants

IG was a right-handed woman, aged 37 at the time of testing. She had suffered from a series of ischemic strokes 8 years earlier, resulting in fairly symmetrical posterior parietal and upper and lateral occipital cortico-subcortical regions (Figure 46). IG had originally presented with simultanagnosia, but this had resolved well before the present experiment (Pisella et al., 2000). IG demonstrated bilateral optic ataxia, with misreaching to targets in extrafoveal vision on either side, with either hand. It has been reported in the literature, that IG has generally accurate reaching movements in central vision (Pisella et al, 2000; Gréa et al., 2002).

Figure 46: A horizontal section through IG's brain, visualized with structural MRI. Extensive damage is present bilaterally in the posterior parietal lobes.



In addition, eleven right-handed adult control participants (8 females and 3 males, mean age: 35 years, range: 25-52 years), with no known visual or motor deficits were also tested. These volunteers were recruited from the staff and Postgraduate students from the Espace et Action laboratory in Lyon, France[2].

Design

The study consists of three blocked fixation conditions, Mid fixation, Left fixation and Right fixation, each presented twice in a Mid, Left, Right, Right, Left, Mid design. Each block was made up of 60 trials, with 6 additional practice trials at the beginning of each block. There were 40 unperturbed trials, in which the target was presented in the central target location, and 20 trials in which the target was perturbed from the central location to a location 65mm to the left (ten trials) or 65mm to the right (ten trials), presented in a pseudorandomised order.

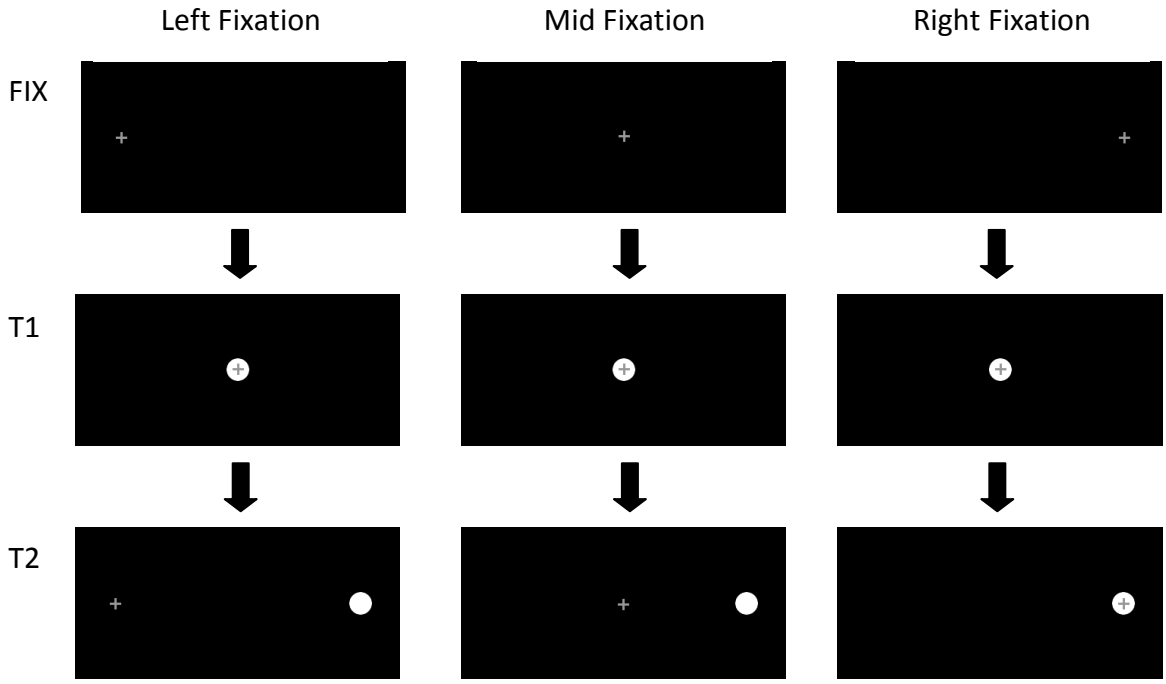
[2] With thanks to Annabelle Blangero

All the blocks require the same biomechanical movements, as the target presentation locations remain the same; it is the fixation location that changes between experimental blocks (see Figure 47). This design of three potential target locations and three fixation conditions allows the investigation of left and right target perturbations from fixation to extrafoveal vision, and also target perturbations to fixation and into the periphery for both the left and right hemifields.

Apparatus

The participant sat at a desk with their left hand resting on their lap and their right-hand index finger resting on the start button (Cambridge Research Systems CT6 response box). Stimuli were presented on a 17" CRT monitor positioned in front of the participant, at a viewing distance of 420mm, in a blacked-out room. The stimulus was a white dot, 10mm in diameter, presented on a black background to reduce glare. As can be seen in Figure 47, each trial began with the presentation of a grey fixation cross (15 x 15 pixels) in either the central, left or right location, depending on the block. On all trials, the target appeared in the centre of the screen when the button was pressed (T1), and either stayed in its initial position (unperturbed trials) or made a jump to 65 mm to the left or right of the central position in the perturbation trials, upon release of the start button (T2). The participant was required to maintain fixation throughout the duration of the trial, with eye movements tracked simultaneously with the hand movements using the ViSaGe system (Cambridge Research Systems) and Optotrak (Northern Digital Inc., Waterloo, Ontario, Canada). One infrared diode was secured to the participants' right index finger, and the kinematic features of the aiming movement were recorded at 200Hz for the duration of 1 second.

Figure 47: Example stimuli of perturbed trials from Experiment 12. The target is the white filled dot and is always presented in the central location on the screen, jumping to the left or the right location in the perturbed trials (only right jumps illustrated). In the unperturbed trials, the T1 stimulus is presented in both the T1 and T2 positions, and so the target does not move from the central location. The three fixation conditions are presented in a blocked design (Mid, Left, Right, Right, Left, Mid).



For IG, a pacing beep was sounded 300ms after movement commencement, with the instruction to touch the dot on the screen in time with the beep. However, her movement times were slower than the paced time and the pacing beep was adjusted to 450ms for the control participants in order to encourage movement times that were similar to those produced by IG. All participants were instructed to keep their finger on the screen until the background turned grey at 1000ms after movement commencement, and then to return their finger to the start button to initiate the next trial.

Procedure

The participants were instructed to maintain fixation on the grey cross throughout the trial. The further instructions are as those detailed in Experiment 1 for the GO condition.

Perceptual Task

Participants were also required to perform a perceptual task after the reaching task had been completed. The participant's task was to discriminate the direction of the target jump and to press the left or right buttons on the response box in reaction to the target jump perceived on screen. The set up for the perceptual task was identical to that of the Reaching task, except for the required response. Once fixation had been established on each trial, the presentation of T1 was initiated by the experimenter. After a delay of 500ms, T1 was replaced by T2, and the participant was required to respond, by pressing the appropriate button the response box for a jump or not responding on the unperturbed trials. The trial ended when a response was made, or timed out after 2000ms.

The design of the Perceptual task blocks was slightly different from the Reaching task, with participants completing six blocks of 45 trials, with 5 practice trials before each block. Each block was made up of 15 unperturbed trials and 30 perturbed trials, with 15 trials to each jump direction, presented pseudo-randomised. Again, as with the Reaching task, fixation condition was blocked and presented in a Mid, Left, Right, Right, Left, Mid design.

Experiment 12: Results

Reaching Task

In the static trials, IG's reaching movements were similar to those made by the control participants and so the use of the two different pacing-beeps generated movements that were well matched for duration and speed. For the static trials, across fixation conditions, IG's movements had a mean duration of 419ms (control mean 453ms, SD 51.96) and a peak speed of 2208mms^{-1} (control mean 2035mms^{-1}, SD 254.69). Crawford and Garthwaite's (2002) modified t-test revealed no significant differences between the pointing performance of IG and the controls for RT, MT, PV or TPV.

IG's endpoint accuracy for static targets was also comparable to that of the controls in the mid fixation condition (IG mean signed angular error 0.27°; control mean 0.04°, SD 0.23) and the right fixation condition (IG mean 0.48°; control mean 0.12°, SD 0.36) and only marginally worse than that of controls in the left fixation condition (IG mean 0.89°; control mean 0.16, SD 0.37; $t = 1.89$; two-tailed $p < 0.1$). However, her optic ataxic misreaching was readily apparent in terms of variable error (standard deviation of signed angular error) in the lateral fixation conditions. IG's variable error was abnormally high in the left fixation (IG mean 1.47°; control mean 0.60, SD 0.09; $t = 9.26$; one-tailed $p < 0.0005$) and right fixation conditions (IG mean 1.64°; control mean 0.68, SD 0.13; $t = 7.07$; one-tailed $p < 0.0005$). She was less precise than controls, though less dramatically so, even in the mid fixation condition, in which the static target was at fixation (IG mean 0.75°; control mean 0.50, SD 0.09; $t = 2.67$; one-tailed $p < 0.05$).

	Fixation	T2	RT	MT	PV	TPV	AE	VE
Controls	Fixate Left	Left	918.18 (287.66)	494.55 (63.26)	2017.91 (256.77)	148.64 (37.29)	0.41 (0.94)	1.45 (1)
		Mid	891.36 (243.33)	447.73 (50.96)	2060.73 (251.62)	151.82 (35.16)	0.16 (0.37)	0.6 (0.09)
		Right	916.82 (264.23)	436.82 (54.65)	2139.95 (229.11)	163.18 (37.23)	-0.08 (0.7)	0.98 (0.36)
	Fixate Mid	Left	940 (292.75)	490.45 (58.11)	1980.66 (306.8)	141.82 (28.92)	0.72 (1.94)	1.62 (0.85)
		Mid	874.55 (258.93)	457.27 (55.51)	2042.88 (283.63)	146.82 (25.52)	0.04 (0.23)	0.5 (0.09)
		Right	880.91 (269.06)	436.36 (53.39)	2162.31 (257.35)	160 (31.14)	-0.32 (1.5)	1.55 (0.88)
	Fixate Right	Left	961.36 (310.78)	483.64 (60.17)	1967.27 (281.8)	153.18 (40.51)	0.71 (1.38)	1.18 (0.6)
		Mid	943.18 (283.01)	453.64 (53.72)	2002.82 (247.1)	158.18 (39.95)	0.12 (0.36)	0.68 (0.13)
		Right	957.73 (281.25)	435.91 (58.98)	2114.56 (226.95)	165.45 (40.28)	-0.6 (1.06)	1.26 (0.84)
IG	Fixate Left	Left	1066.32 (441.3)	440.00 (68.96)	2226.45 (201.71)	111.05 (17.61)	7.18 (1.86)	1.86
		Mid	940.25 (189.37)	428.00 (35.73)	2239.19 (222.74)	112.13 (20.54)	0.89 (1.47)	1.47
		Right	964.44 (250.96)	417.78 (19.87)	2259.89 (161.89)	110.00 (17.15)	-4.97 (2.03)	2.03
	Fixate Mid	Left	759.00 (239.67)	468.50 (35.88)	2208.30 (178.38)	107.00 (16.89)	4.38 (1.87)	1.87
		Mid	851.77 (321.41)	433.80 (31.14)	2284.98 (213.99)	109.62 (18.77)	0.27 (0.75)	0.75
		Right	790.00 (248.45)	428.00 (53.57)	2178.79 (213.55)	110.00 (18.92)	-2.59 (2.21)	2.21
	Fixate Right	Left	906.00 (265.14)	443.00 (49.43)	2124.71 (178.94)	112.50 (18.6)	5.82 (1.87)	1.87
		Mid	902.95 (335.13)	429.23 (57.86)	2170.92 (222.16)	113.33 (42.39)	0.48 (1.64)	1.64
		Right	867.37 (256.4)	410.00 (31.09)	2187.85 (183.17)	112.63 (19.96)	-5.04 (2.21)	2.21

Table 27: Means for the unperturbed (mid fixation) and corrected perturbed (left and right) trials for each of the dependent variables, RT, MT, PV, TPV, AE and VE (standard deviations given in brackets) for the control participants and IG.

The high variability in IG's pointing performance validates the use of cut-offs based on average control performance, which are plotted through the lower-cut

offs for normality (one tailed $p < 0.05$) calculated at each time point according to the method of Crawford & Garthwaite (2002). As can be seen in Figure 48, the horizontal spread of the responses to the static middle target has implications for the bandwidth that is calculated from these responses in order to classify the perturbed trials as corrected or not. If the bandwidth had been calculated for each individual's static trial performance, then the bandwidth for IG would have been more conservative than the bandwidth used for the control data, limiting the ability to detect all of the corrections made. Therefore, the data presented here are liberal estimates of IG's correction rates, due to the average control performance bandwidth.

Although the data processing technique used could potentially overestimate the rates of corrections, the rates produced by IG were very low, especially in the lateral fixation conditions. For the left fixation condition, IG's movements towards a left jumping target were corrected on 21% of trials (control mean 93%, range 80-100) and 22% for a right jumping target (control mean 100%, range 100-100). For the right fixation conditions, IG corrected towards a left jump on 35% of trials (control mean 96%, range 80-100) and towards a right jump on 32% of trials (control mean 93%, range 75-100). In the mid-fixation conditions, IG produced higher rates of corrected trials, with 65% for leftwards jumps (control mean 89%, range 40-100) and 90% for rightward jumps (control mean 92%, range 55-100), yet this does not imply her performance was similar to controls. As can be seen from Figure 48, the corrections that were made in the mid-fixation condition were very small in amplitude, and as Figure 49 demonstrates, the classification of a trajectory as a correction does not indicate the latency at which the correction was made, which can be established by plotting rates of correction as a function of time since target jump.

Figure 48: Endpoints of reaching movements for one representative healthy control participant (left) and patient IG (right), for the left fixation (top), mid fixation (middle) and right fixation (bottom) conditions. In each plot, data are separated on the ordinate according to target 2 location: left (jump left), mid (static trials) or right (jump right). The vertical lines indicate the lateral location of left, mid and right targets, and the heaviest vertical line in each plot corresponds to the location fixated. For jump trials, unfilled circles indicate endpoints classed as uncorrected, and filled triangles indicate those classed as corrected.

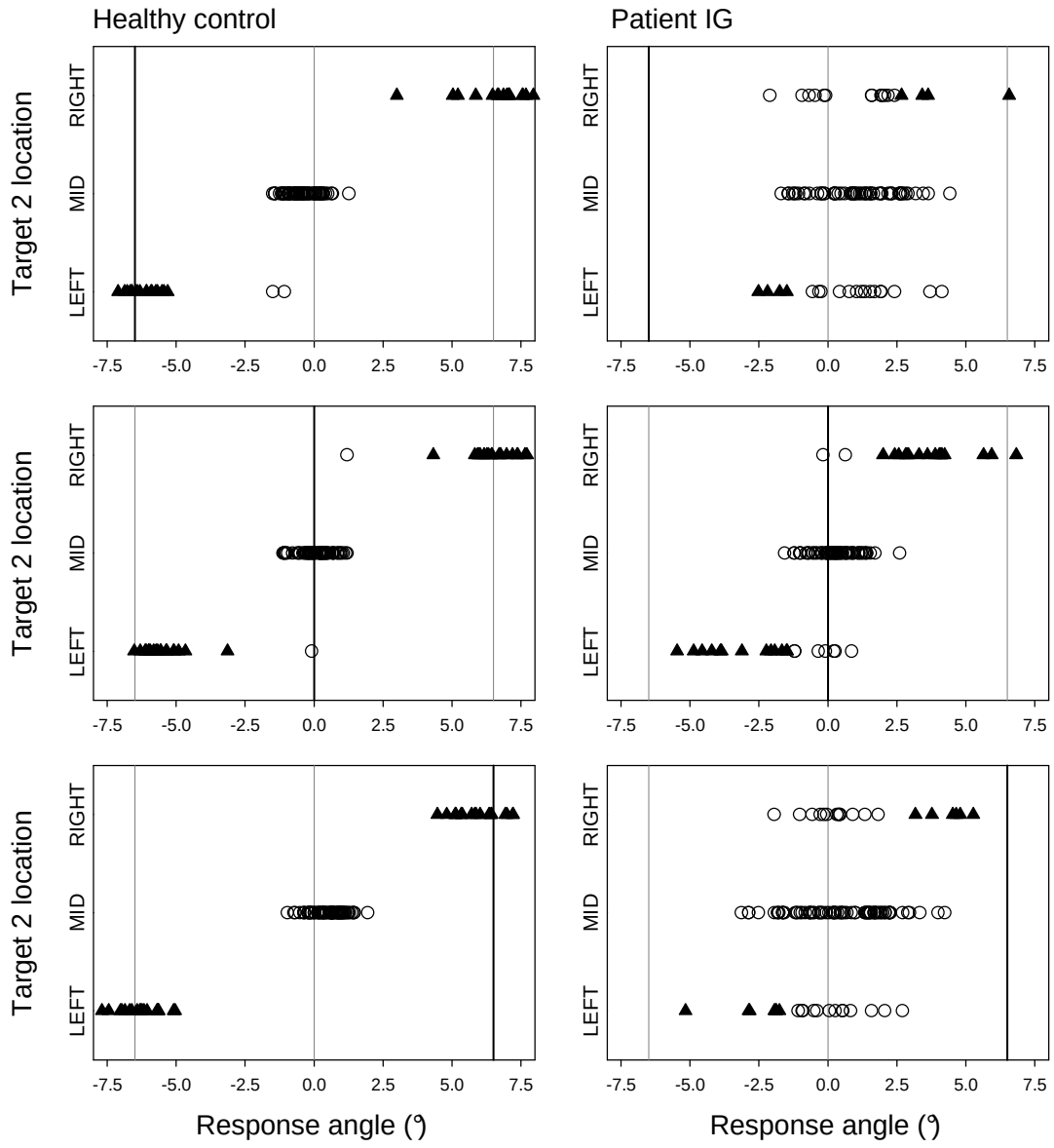


Figure 49: Percentage movements corrected against time from target jump for the healthy control group (left) and patient IG (right), in left fixation (top), mid fixation (middle) and right fixation (bottom) conditions. Solid lines represent observed correction rates, and dotted lines the best fitting straight lines through the lower normal cut-off for corrections (one-tailed) (Crawford and Garthwaite, 2002). Black lines relate to jump right, and grey lines to jump left trials. Note that these profiles reflect the number of movements classified as corrected at each point in time expressed as a proportion of the total number of movements ongoing at that time. These are therefore not cumulative rates of correction, but separate estimates of correction rate for each represented time. The plots do not extend beyond 450 ms because too few movements were represented beyond this time to allow reliable estimates of correction rate. Accordingly, the final rate of correction plotted here (at 450 ms) does not necessarily correspond to the terminal correction rates estimated from movement endpoints.

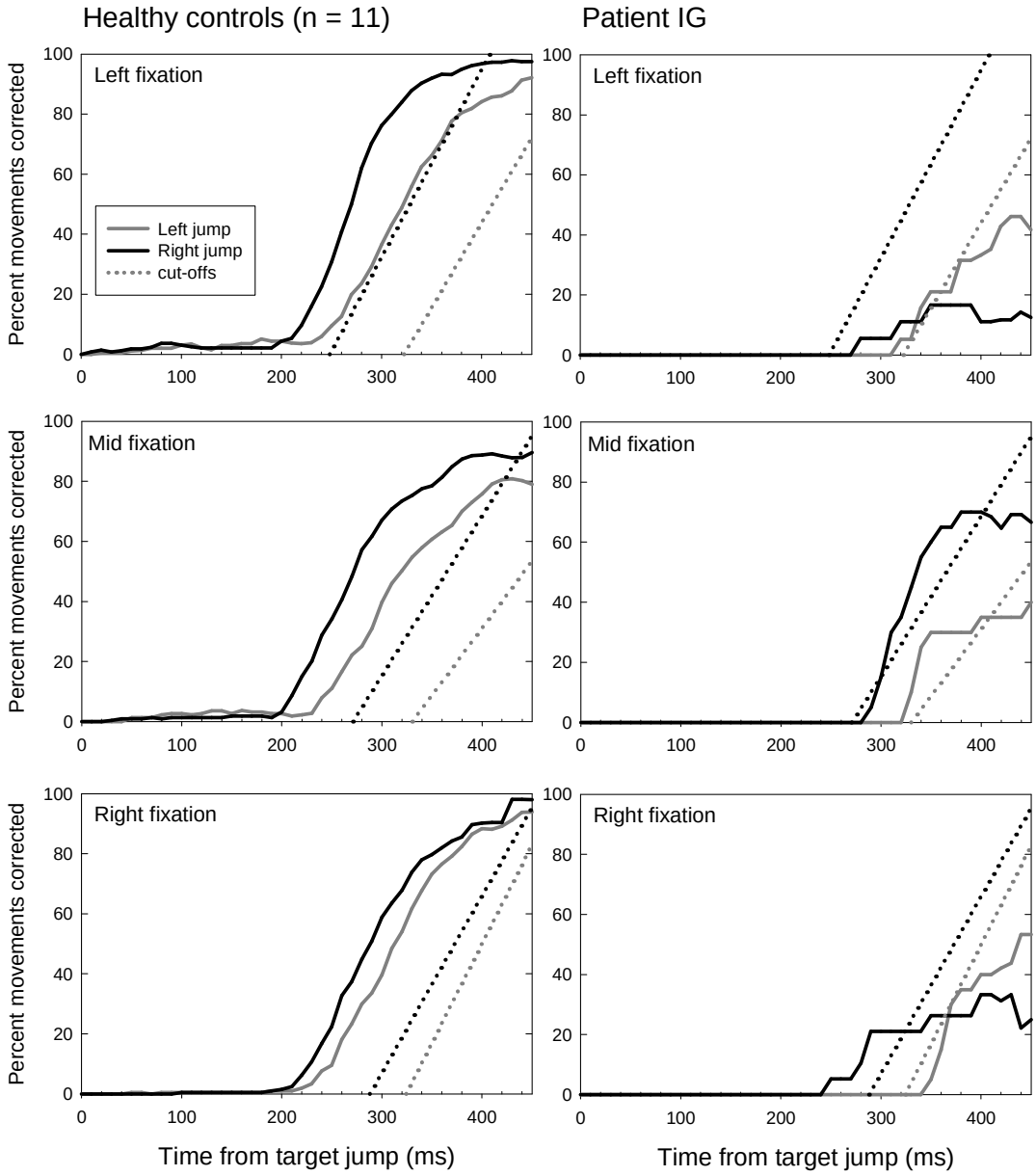


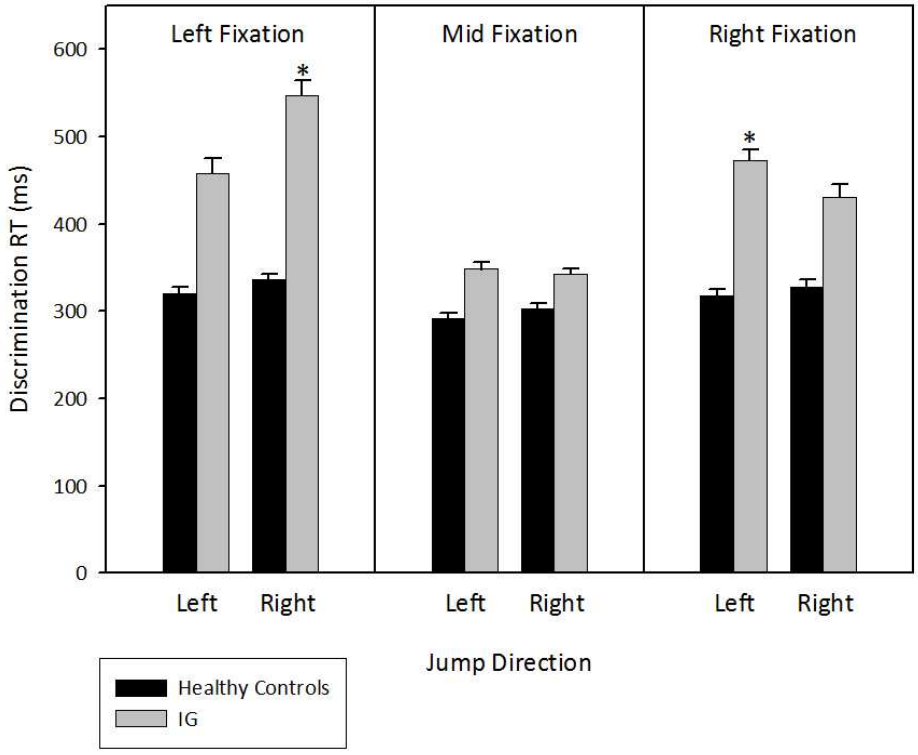
Figure 49 shows the development of correction rate over time in each fixation and jump condition for the control group and for patient IG. In all conditions, IG's performance is clearly abnormal. Whilst corrections can be identified in the hand paths of controls from around 200 ms for a right jump and 220 ms for a left jump, IG's earliest corrections emerge around 100 ms later than this. As well as illustrating her universal lack of fast online corrections (Pisella et al, 2000), Figure 49 confirms that IG's performance is poorest in the lateral fixation conditions. The absence of any benefit in when the target jumps to the point of fixation (i.e. left fixation, jump left; right fixation, jump right) refutes the simple hypothesis that the online correction deficit depends solely upon the location towards which the correction is required.

Perceptual Task

All participants detected the direction of target jump with high accuracy and made few false alarms on static trials (total errors for IG: 2; control range 0-6). Reaction times, trimmed for outliers (> 2SD from the mean per participant), are shown in Figure 50 for IG and the control group.

The first point to note is that IG responded similarly to controls in the mid fixation condition, indicating that the slowness of her trajectory corrections in the equivalent reaching condition did not result from a delay in perceptual detection of the target jump, or discrimination of its direction. However, she was significantly slower than controls to discriminate target jumps from an extrafoveal location (8.8°) to the periphery (17.6°) (left fixation, right jump; right fixation, left jump). In both cases, one-tailed comparison of IG's performance against that of the control group was significant at $p<0.05$ (Crawford and Garthwaite, 2002). This suggests a perceptual weakness affecting peripheral vision in IG, but which does not account for her universally absent online correction.

Figure 50: Mean reaction time (RT) of patient IG (grey bars) and healthy controls (black bars) to report the direction of target jump in the discrimination task. *=p<0.05 one-tailed comparison of IG's performance against the control group (Crawford and Garthwaite, 2002).



Summary

IG's reaching task performance was poorer than that of the control participants. She was less precise than the controls when pointing in central vision, but more precise in central vision than in the left or right fixation conditions, where her error rates were abnormally high. IG produced abnormally low rates of correction, in comparison with the controls and did not benefit from the target jumping to fixation. IG's correction impairment appears to cover her central vision too, and her reaching and correction abilities seem to be functionally distinct. The findings from the perceptual task refute the possibility that IG's poor correction ability is due to not detecting the new location of the perturbed target, as her performance was within the normal limits in the mid-fixation condition. However, IG was slower to react to targets that were perturbed to the

extrafoveal locations from the periphery, and across both the reaching and perceptual tasks performance deteriorated with target eccentricity.

Experiment 12: Discussion

The aim of this experiment was to test whether the online correction deficit in optic ataxia could be explained as a manifestation of the general misreaching deficit widely described in the literature, whereby correction performance is impaired by the extrafoveal target location. It was predicted that bilateral optic ataxic patient IG would not make fast corrections for targets jumped to extrafoveal locations, but would do so for targets jumped to her point of fixation. IG's reaching to static targets confirmed the sensitivity of her misreaching to retinal eccentricity, in that her performance deteriorated for extrafoveal targets in the lateral fixation conditions, in comparison with foveal targets in the mid fixation condition. However, her online correction abilities did not similarly depend on the location to which the target was jumped. Fast corrections were universally absent for IG and, most critically, there was no benefit when the target jumped to her point of fixation. This refutes the tested hypothesis, and implies that the location to which the movement is *initially* directed is important in determining the online correction deficit in optic ataxia.

The present study confirms and extends Pisella et al.'s (2000) demonstration of an online deficit in patient IG, and the perceptual discrimination task supports the conclusion that this deficit is not secondary to impaired perceptual awareness of the target jump. In Pisella et al.'s (2000) original study, this was suggested by the normal latency with which IG reacted when required to stop her movement upon detection of a target jump. In the present study, we required IG to discriminate the *direction* of the jump, which could not be achieved simply by detecting the offset of the first target. In the mid fixation

condition, she made this discrimination as quickly as control participants, which supports the idea that a general attentional deficit does not explain her online correction deficit. IG's perceptual discriminations were, however, slowed in the lateral fixation conditions when the target jumped to the most eccentric locations. This adds to the evidence for peripheral deficits of visual attention in patients with optic ataxia (Michel & Henaff, 2004; Striemer et al, 2007, 2009). Attentional deficits may not cause optic ataxia (cf. Striemer et al, 2009), but they may nonetheless influence the visuomotor behaviour of such patients. In IG, for instance, impaired perceptual awareness of the target jump does not explain the absence of fast automatic corrections, but it may shape the pattern of her later voluntary corrections.

Experiment 12 has demonstrated that IG's poor correction abilities are not related to the final location of the perturbed target, implicating the initial target location as an important factor. Initial reach direction is thought to be important because in order for online correction to be accurate, there needs to be a simultaneous representation of the current hand position and the new target location. Thus, if optic ataxia involves an impaired representation of extrafoveal locations for action, it might also affect the representation of ongoing extrafoveal reaches. If the hand is reaching towards a central, foveated location, and the target location is perturbed into the periphery, the current hand position will be represented, but there will be no representation of the new target location. Conversely, if the hand is reaching towards a peripheral reach and is diverted towards a central target at fixation, the new target location may be represented, but the hand position may not be, hence the failure to produce accurate corrections.

Furthermore, in the light of the findings from Experiment 9, the spatial relationship between the target position (i.e. the hemifield) and the hand could also be an influencing factor, with the direction of the perturbation driving the deficit. It would be suggested that bilateral optic ataxic participants would be

impaired in making contralesionally-directed movement corrections in any part of the visual field, if the dorsal stream in each hemisphere differentially sub-serves contralaterally-directed corrections. However, in a bilateral participant, like IG, it is not possible to distinguish between these two accounts, and a more definitive test would be to run the same experiment with a unilateral optic ataxic. Experiment 13 is conducted with a unilateral optic ataxic patient, CF, with field-dependent misreaching (Blangero et al., 2008) to allow the dissociation of the direction of the target jump from the involvement of the ataxic field.

The first, positional explanation would predict that CF should fail to correct when a target jumps from the ataxic field to the point of fixation, because the initial position is in the impaired field, but not when it jumps from the non-ataxic field to the point of fixation. The second, directional hypothesis would predict the opposite, as the former case requires a correction towards the ipsilesional side, and so should be preserved, whilst the latter requires a correction towards the contralesional side, and so should be impaired.

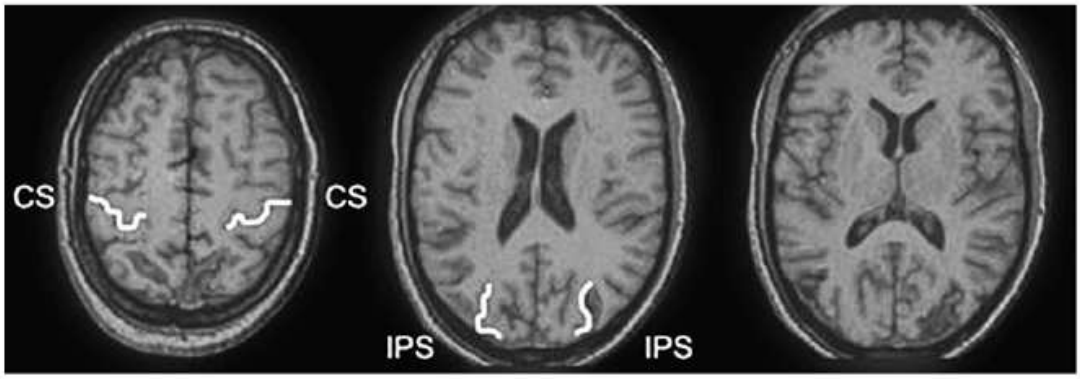
Experiment 13: Methods

Participants

CF is a right-handed male, who suffered a bilateral watershed posterior infarct at the age of 24. CF has asymmetrical bilateral lesions of the parieto-occipital region, which are larger in the right hemisphere, affecting Broadman's areas 18, 19, 7, 5, and 2. At the time of testing, CF, aged 28 years, displayed optic ataxia with his left hand in the left visual field, and no visual field deficits were reported. Blangero et al. (2008) report that CF had no ataxia for targets

presented in central vision, no sign of hemispatial neglect and no motor, somatosensory or visual deficits.

Figure 51: CF's MRI showing asymmetrical bilateral lesions of parieto-occipital regions (Broadmann's areas 18, 19, 7 and 5). (Image and wording from Blangero et al., 2008)



The same eleven control participants, as described in Experiment 12, were used in the comparison of CF's data.

Design

The design of the experiment is the same as detailed in Experiment 12. One exception is that CF was tested in the reaching task with his right (non-ataxic) hand for two blocks (Mid, Left, Right, Right, Left, Mid), and his left (ataxic) hand for one block (Mid, Left, Right). Only the data from his non-ataxic right hand is presented.

Apparatus

The apparatus used in the current experiment is the same as detailed in Experiment 12.

Procedure

The procedure is the same as detailed in Experiment 12 for the reaching and the perceptual discrimination tasks.

Experiment 13: Results

Reaching Task

CF performed similarly to controls in terms of the movement kinematics. For static trials across the fixation conditions, CF's movements had a mean duration of 502ms (control mean 453ms, SD 51.96) and a peak speed of 2100 mms^{-1} (control mean 2035mms^{-1}, SD 254.69). Crawford and Garthwaite's (2002) modified t-test revealed no significant differences between the pointing performance of CF and the controls for RT, MT, PV or TPV.

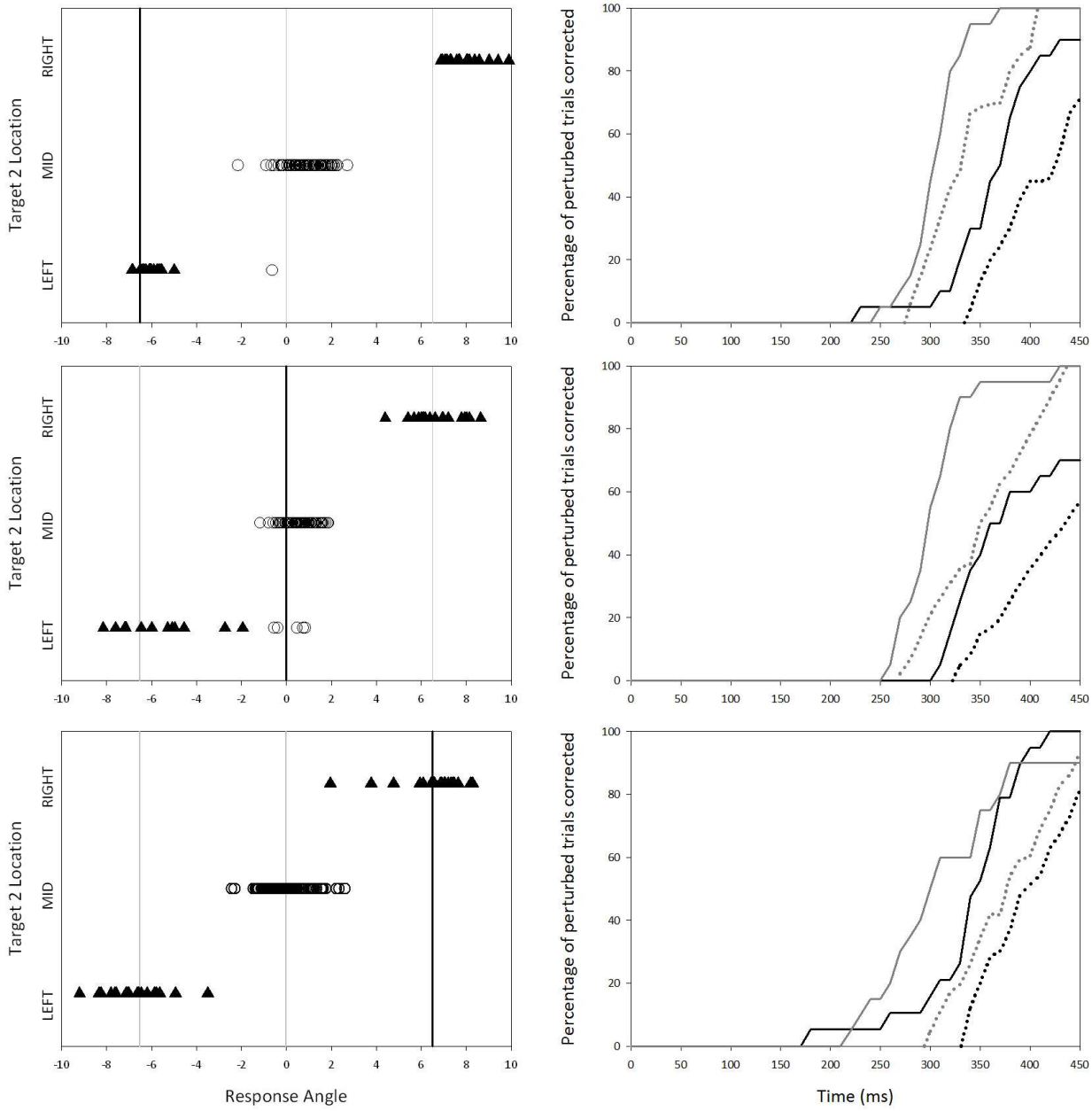
CF's endpoint accuracy for static targets was also comparable to that of the controls in the right fixation condition (CF mean signed angular error 0.05°; control mean 0.12°, SD 0.36), but became marginally worse at mid fixation (CF mean 0.55°; control mean 0.04°, SD 0.23; $t = 2.12$; two-tailed $p < 0.05$) and in the left fixation condition (CF mean 0.95°; control mean 0.16, SD 0.37; $t = 2.38$; two-tailed $p < 0.05$). The analysis variable error, revealed a significantly wider spread of errors in the static trials for each of the fixation conditions (Left fixation: CF mean 0.84°; control mean 0.60, SD 0.09; $t = 2.55$; one-tailed $p < 0.01$; Mid fixation: CF mean 0.69°; control mean 0.50, SD 0.09; $t = 2.02$; one-tailed $p < 0.05$; Right fixation: CF mean 1.02°; control mean 0.68, SD 0.13; $t = 2.50$; one-tailed $p < 0.01$), than was observed in the control performance.

Fixation location	T2 location	RT	MT	PV	TPV	AE	VE
Fixate Left	Left	460.55 (59.33)	560.5 (41.86)	2149.75 (239.35)	171 (20.49)	0.67 (1.3)	1.3
	Mid	442.11 (77.22)	506.38 (42.52)	2099.16 (221.82)	178.88 (28.42)	0.95 (0.84)	0.84
	Right	454.25 (77.26)	471 (67.74)	2130.62 (204.28)	177 (36.58)	1.66 (1.14)	1.14
Fixate Mid	Left	549.75 (89.26)	535 (37.91)	2046.21 (250.13)	179.5 (27.81)	2.23 (3.07)	3.07
	Mid	583.18 (195.74)	501.38 (46.98)	2075.26 (288.54)	183.63 (43.9)	0.55 (0.69)	0.69
	Right	617.3 (191.3)	463.5 (33.76)	2156.71 (182.21)	192.5 (37.54)	0.19 (1.06)	1.06
Fixate Right	Left	525.26 (122.87)	538.95 (32.64)	2103.82 (134.23)	172.63 (14.85)	-0.3 (1.33)	1.33
	Mid	490.77 (81.08)	498.35 (33.98)	2126.37 (129.94)	176.08 (15.39)	0.05 (1.02)	1.02
	Right	513.2 (112.5)	507 (58.86)	2123.22 (103.78)	182 (15.42)	-0.03 (1.51)	1.51

Table 28: Means for the unperturbed (mid fixation) and corrected perturbed (left and right) trials for each of the dependent variables, RT, MT, PV, TPV, AE and VE (standard deviations given in brackets) for CF. Control participants data is displayed in Table 27.

CF's pointing performance was classified using the same bandwidth as outlined in Experiment 12, and as can be seen in Figure 52, CF produced a high rate of corrections across all fixation conditions. CF produced 100% corrections for a rightward target location perturbation in all three fixation conditions, and in the leftwards jump trials, CF corrected on 95% of trials in the left fixation, 75% in the mid fixation and 100% in the right fixation conditions. This high correction rate was accompanied by accurate endpoints in the left fixation condition, due to all stimuli being presented in CF's non-ataxic hemifield, with marginally decreasing performance in the mid fixation and then the right fixation condition, as illustrated in Figure 52. In the mid fixation condition, CF produced his most accurate static trial pointing, but he produced less accurate corrections towards leftwards jumping targets. In the right fixation condition, and thus when performing in his ataxic field, CF was slower to initiate the corrections but still performed well in reaching to both left and right jumps.

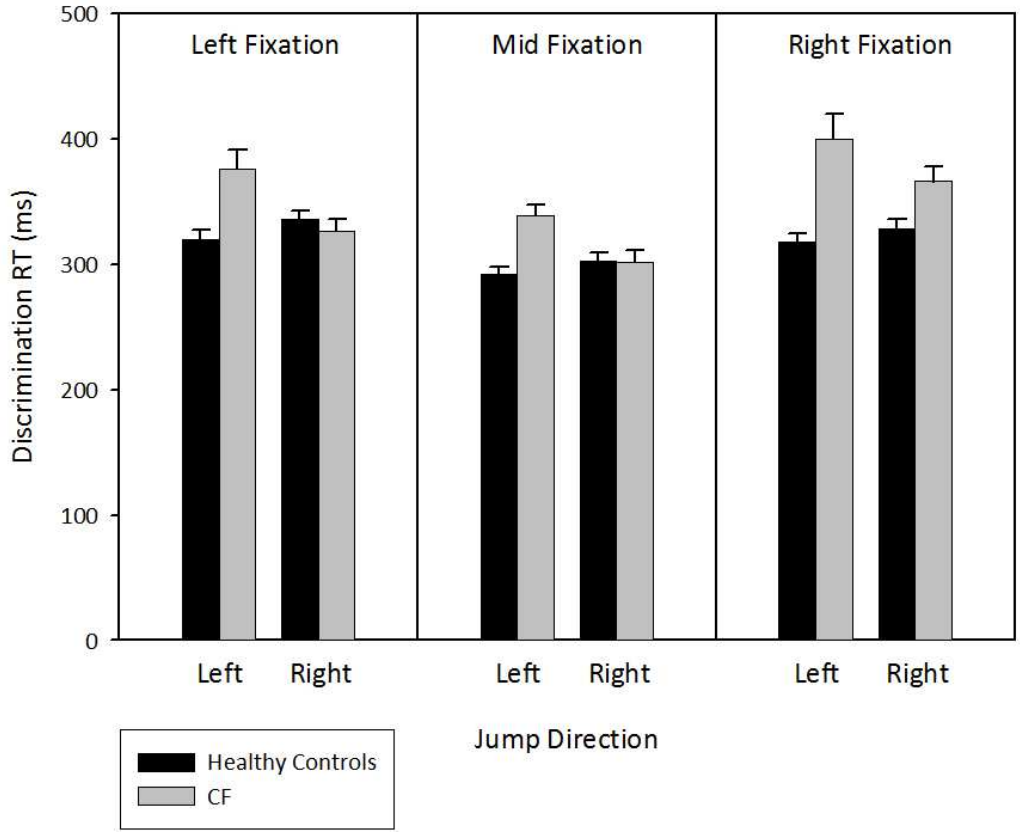
Figure 52: Endpoints of reaching movements and percentage of perturbed trials corrected for patient CF for the left fixation (top), mid fixation (middle) and right fixation (bottom) conditions. Black line is the left hand and the grey line is for the right hand. For further detail, see Figures 48 and 49.



Perceptual Task

CF performed as well as controls in the perceptual discrimination task, as Figure 53 shows.

Figure 53: Mean reaction time (RT) of patient IG (grey bars) and healthy controls (black bars) to report the direction of target jump in the discrimination task. There was no significant difference in performance between CF and the control participants.



Summary

In this task, CF's optic ataxia was not as evident as expected. It was predicted that CF would have difficulty with leftward target location perturbations, and all target jumps in the right fixation condition. These difficulties did not show up in the analysis and CF was able to produce a high rate of corrections across all

fixation conditions. CF also performed as well as controls in the perceptual discrimination task across all fixation conditions.

Experiment 13: Discussion

Experiment 13 attempted to differentiate between explanations for the findings of Experiment 12, and the influence of the original target location in the successful execution of online corrections. It was not possible to distinguish between the two hypotheses considered, as CF failed to demonstrate the expected pattern of deficits. It was predicted that CF would have difficulty with all target jumps in the right fixation condition, as although he has a bilateral lesion, he has a larger lesion in his right hemisphere and has been demonstrated in the literature to have optic ataxia with his left hand and in the left visual field (Blangero et al., 2008; Kahn et al., 2005; Striemer et al., 2007).

Although the corrections took longer to initiate, CF was still able to produce 100% corrections to a target that jumped from his periphery to an extrafoveal location within his ataxic hemifield. This unexpected result may have been due to the small (8°) amplitude of the target jumps in this experiment. In a patient such as IG, Rossetti et al. (2005) had to perturb the target to 23° to demonstrate large errors in IG's performance, yet, in Experiment 12, IG's error rates were rather large with the same set experimental set up as that used with CF, and a similar design had appeared to be very sensitive to MH's difficulties in Experiment 11. Furthermore, Blangero et al. (2008) reported significant hand and field effects in CF's ability to correct to a target perturbed 10°, and described how the pattern mirrored his misreaching deficit to stationary targets.

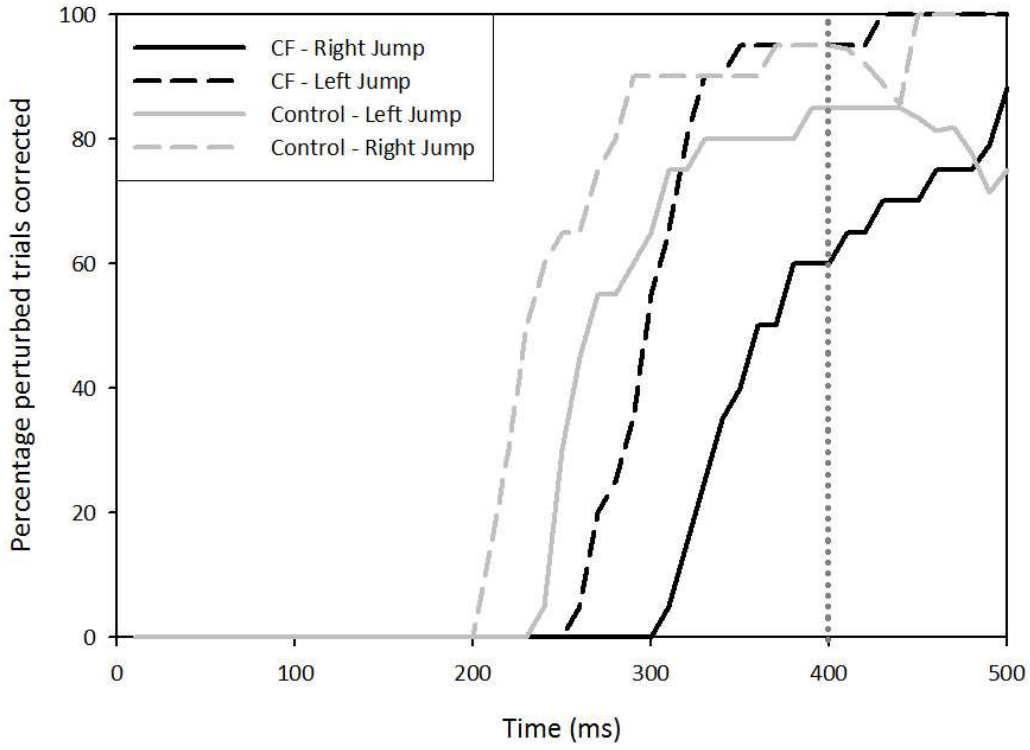
The current experiment however, failed to observe a considerable field effect and did not record dramatic pointing errors, so unless CF's optic ataxia had disappeared over time, there is a need to explain these discrepancies in the findings of the current experiment and the Blangero et al. (2008) study. One possible explanation is the control of MT in the Blangero et al. (2008) study. Blangero et al. (2008) did not report CF's MT, and there is no detail in the article about how the desired MT was illustrated or whether feedback was given if any participant was moving too slowly. Furthermore, it does not appear that Blangero et al. (2008) excluded any trials in which CF moved slower than 400ms. In the current experiment, CF was encouraged to reach towards the screen in time with a 300ms pacing beep, but his MTs were ~500ms, even though he was instructed to move as fast as possible. Therefore it is possible that Blangero et al. (2008) were sampling CF's movements at a later time point than controls, and thus selecting a different part of the trajectory, as illustrated in Figure 54.

In Experiments 1, 3, 4 and 9, in the current thesis, where there were bidirectional perturbations, there was an observed difference in the corrections produced towards left and right perturbed targets. The same pattern is evident in CF's data in the current experiment (see Figure 52), with higher rates of corrections to the right. This pattern is not observed by Blangero et al. (2008) in their control data, and could be misleading in supporting the finding of a hand effect in the optic ataxic participant.

As illustrated in Figure 52, there is a difference between correction rate performance for reaches towards the left and the right for both the control participant (grey lines) and CF (black lines) in the mid fixation condition of the current experiment. There is also a noticeable difference in the latency of the corrections made by the two participants and in the rate in which they increase. The corrections by the control participant show up earlier in the spatial analysis, than do those made by CF, and accumulate quickly to a high rate. If you

were to sample these trajectories at a 400ms endpoint cut-off (grey dotted line), then the differences between the jump direction is more apparent in CF, as it is earlier in the trajectory, and the left/right asymmetry is not as noticeable in the controls. This could lead to the conclusion that there is a deficit in the correcting behaviour of one hand in comparison to the other. Kinematic analysis allows for sampling at a number of time frames, and thus adds power to the analysis of the ongoing trajectories.

Figure 52: Percentage of perturbed trials corrected plotted by time in ms for Patient CF (black lines) and for a representative control participant (grey lines). The dotted grey line at 400ms is an example to the cut-off used by Blangero et al. (2008).



As stated at the beginning of the discussion, the aim of Experiment 13 was to disentangle the relationship between online correction and misreaching in a unilateral optic ataxic patient, following on from bilateral optic ataxic patient IG. Although CF presented with unilateral symptoms, he had bilateral brain lesions, and although the results of Experiment 13 are interesting, they are inconclusive

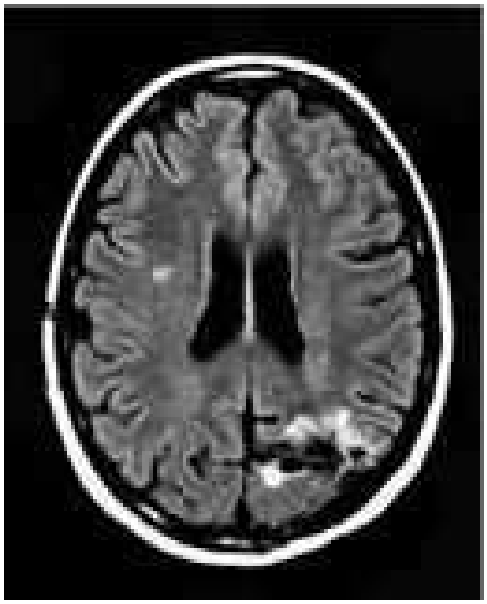
with regard to the experimental aim. Experiment 14 was run using the same experimental set up but with a unilateral optic ataxic patient with unilateral brain lesions.

Experiment 14: Methods

Participants

Patient ML is a left-handed female, aged 60years old at the time of testing. She suffered a haemorrhagic stroke in the right hemisphere, 16 years prior to testing. The lesion damaged the parieto-occipital junction and the caudal part of the intraparietal sulcus and of the superior parietal lobule. Following this focal lesion, ML exhibited optic ataxia symptoms isolated to the left visual field using both hands. The same eleven control participants, as described in Experiment 12 were used in the comparison of ML's data.

Figure 55: A horizontal section through ML's brain, visualized with structural MRI. Extensive damage is present unilaterally in the parieto-occipital junction.



Design

The design of the experiment is the same as detailed in Experiment 12.

Apparatus

The apparatus used in the current experiment is the same as detailed in Experiment 12.

Procedure

The procedure is the same as detailed in Experiment 12.

Experiment 14: Results

ML performed similarly to controls in terms of the movement kinematics. For static trials across the fixation conditions, ML's movements had a mean duration of 435ms (control mean 453ms, SD 51.96) and a peak speed of 1992 mms^{-1} (control mean 2035mms^{-1}, SD 254.69). Crawford and Garthwaite's (2002) modified t-test revealed no significant differences between the pointing performance of ML and the controls for RT, MT, PV or TPV.

ML's endpoint accuracy for static targets was also comparable to that of the controls in the mid fixation condition (ML mean signed angular error 0.05°; control mean 0.04°, SD 0.23), the right fixation condition (ML mean -0.27°; control mean 0.12°, SD 0.36), and in the left fixation condition (ML mean -0.09°; control mean 0.16). The analysis variable error, revealed a significantly wider spread of errors in the static trials for the lateral fixation conditions, especially in the fixate right condition (Left fixation: ML mean 0.77°; control mean 0.60, SD 0.09; $t = 1.81$; one-tailed $p < 0.05$; Right fixation: ML mean 1.29°; control mean

0.68, SD 0.13; t = 4.49; one-tailed $p < 0.001$), than was observed in the control performance. Mid fixation static trial performance was similar to controls (ML mean 0.58°; control mean 0.50, SD 0.09), in terms of endpoint accuracy, yet the correction performance looks very different, as illustrated in Figure 56. Furthermore, ML was significantly inaccurate when reaching towards a rightwards perturbed target in both the lateral fixation trials (Left fixation, Right jump: ML mean 3.02°; control mean 0.98, SD 0.36; t = 5.53; one-tailed $p < 0.001$; Right fixation: ML mean 2.96°; control mean 1.26, SD 0.84; t = 1.94; one-tailed $p < 0.05$)

Fixation location	T2 location	RT	MT	PV	TPV	AE	VE
Fixate Left	Left	808.5 (399.03)	484 (74.15)	2082.27 (231.83)	127.5 (24.89)	2.31 (2.79)	2.79
	Mid	923.38 (417.47)	420.91 (40.53)	2088.23 (353.54)	117.92 (70.25)	-0.27 (0.77)	0.77
	Right	902.63 (408.97)	448.95 (53.63)	2042.95 (278.54)	130 (36.06)	-1.14 (3.02)	3.02
Fixate Mid	Left	787 (234)	612 (81.49)	1744.11 (367.6)	160 (83.67)	0.37 (1.06)	1.06
	Mid	870 (503.28)	460.45 (46.8)	1881.2 (333.72)	152.05 (55.64)	-0.05 (0.58)	0.58
	Right	836.67 (571.62)	438.89 (32.19)	2188.29 (391.13)	126.67 (46.37)	-0.11 (1.03)	1.03
Fixate Right	Left	952.86 (475.28)	470 (44.94)	2011.21 (157.35)	125.24 (31.72)	2.78 (1.72)	1.72
	Mid	892.33 (390.87)	426.03 (36.16)	2005.69 (209.48)	118.49 (35.89)	-0.09 (1.29)	1.29
	Right	1036.5 (328.04)	499 (87.23)	1919.84 (228.63)	146 (60.12)	-1.45 (2.96)	2.96

Table 29: Means for the unperturbed (mid fixation) and corrected perturbed (left and right) trials for each of the dependent variables, RT, MT, PV, TPV, AE and VE (standard deviations given in brackets) for ML. Control participants data is displayed in Table 27.

ML's pointing performance was classified using the same bandwidth as outlined in Experiment 12, and as can be seen in Figure 56, ML produced a high rate of

corrections across all fixation conditions. ML produced 100% corrections for both left and right target perturbations in the mid fixation condition, 90% corrections towards both directions in the Right fixation condition and 80% for left jumps when fixating left and 84% for right jumps when fixating left. Yet accompanying this high rate of corrections is a clear field effect in the mid fixation condition. Although the endpoint data look precise, the timing of the corrections is very different for reaches towards the left and right new target locations, with impaired corrections in the left hemifield. ML's correction performance is poorer when fixating right and the stimuli are presented in her ataxic left-hemisphere, although ML still produces a high rate of correction, and still performs within the control cut-offs.

Perceptual Task

ML's performance on the perceptual discrimination task was slower than controls. As can be seen in Figure 57, ML is significantly slower in the mid fixation trials (Left jump: ML mean 528ms; control mean 292ms, SD 82; $t = 2.76$; one-tailed $p < 0.01$; Right jump: ML mean 477ms; control mean 303, SD 79; $t = 2.11$; one-tailed $p < 0.05$) and when the target jumped to the left when fixating right (ML mean 577ms; control mean 318ms, SD 85; $t = 2.92$; one-tailed $p < 0.005$). In this condition, the target would have jumped to the most eccentric target location in her ataxic hemifield, and a delay in responding would be expected. The overall slowness in responding in the perceptual task however, has no baring on her correction latencies, which fell within the normal range (see Figure 56), demonstrating a difference between the two types of task.

Figure 57: Mean reaction time (RT) of patient IG (grey bars) and healthy controls (black bars) to report the direction of target jump in the discrimination task. *=p<0.05 one-tailed comparison of IG's performance against the control group (Crawford and Garthwaite, 2002).

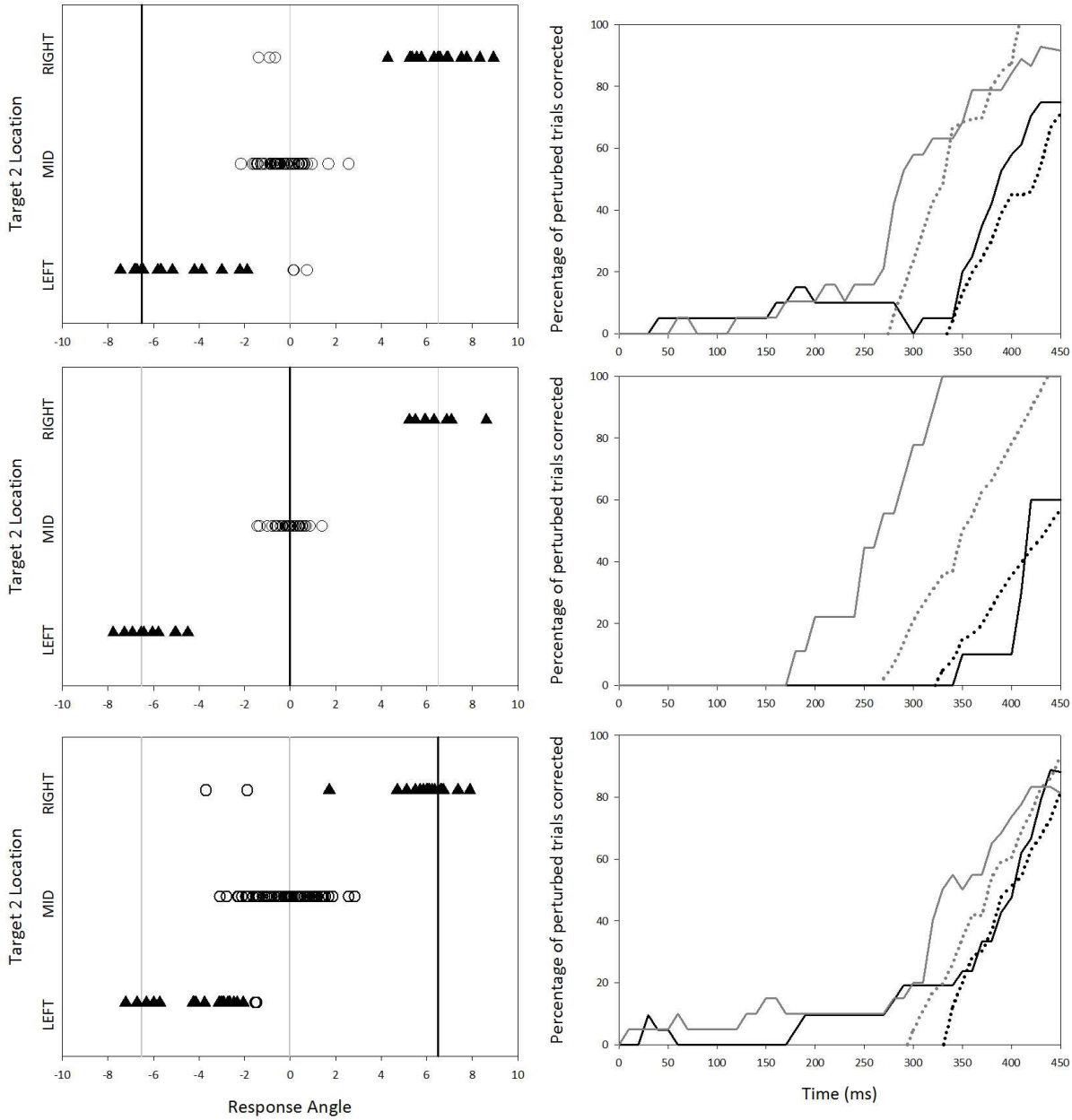
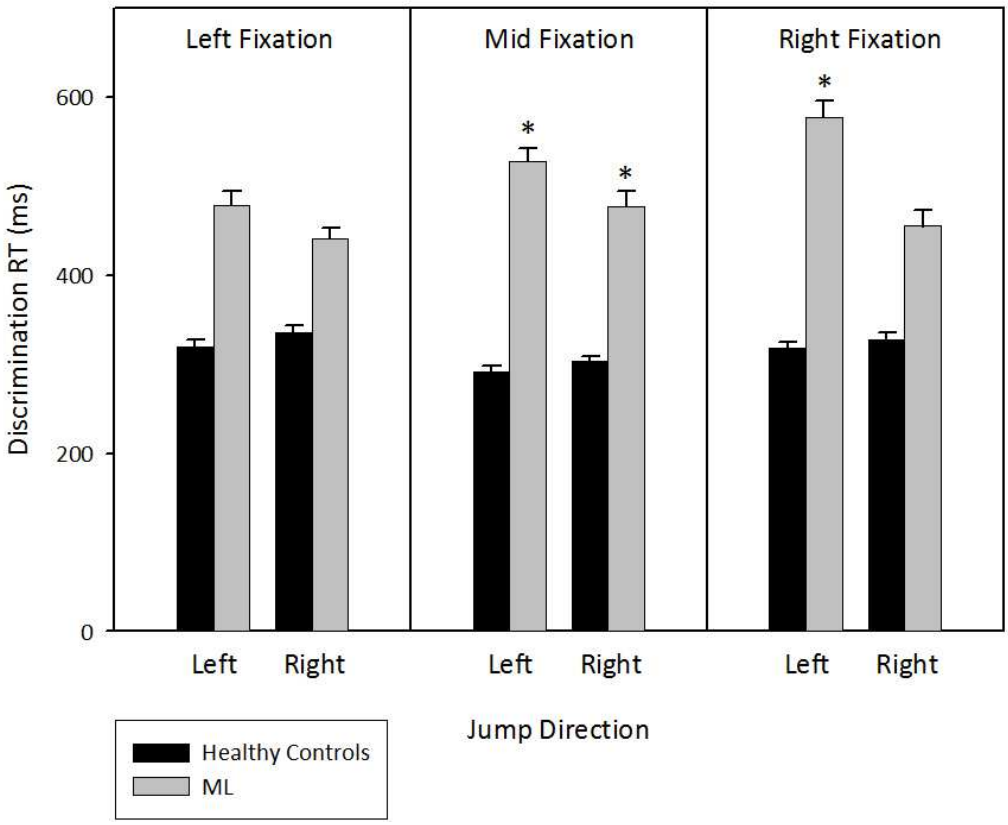


Figure 56: Endpoints of reaching movements and percentage of perturbed trials corrected for patient ML for the left fixation (top), mid fixation (middle) and right fixation (bottom) conditions. Black line is the left hand and the grey line is for the right hand. For further details, see Figures 48 and 49.



Summary

ML's performance on this double-step task demonstrated the more classic symptoms of optic ataxia. Her static pointing performance in the mind fixation trials was comparable to controls, with high levels of accuracy. The rate of errors began to increase with the requirement to fixate laterally, and to point to more eccentric target locations, yet the rate of corrections remained quite high. ML was able to produce corrections with a latency that fell within the cut-off calculated from the control participant performance, except for in the mid fixation condition towards a leftward jumping target. In this condition, ML was unable to make fast corrections towards the new target location.

Experiment 14: Discussion

ML provided the opportunity to test the hypothesis of whether the deficit in online corrections that has been well established in the optic ataxic literature, is a manifestation of the more general misreaching deficit or is specific to online control and reflects a 'faulty automatic pilot'. The findings from Experiment 14 appear to refute the extrafoveal hypothesis, as for ML, the jump direction and the original location of the target have an impact on her ability to correct towards a target location perturbation.

The leftwards jump in the mid fixation condition produced a very pronounced field effect, and poorer performance compared to the right jump in the left fixation condition, where the target was perturbed to fixation. ML's online corrections struggled in the right fixation condition, where all targets were presented within her ataxic hemifield, and thus, the left jump matters for ML, thus appearing to provide support for the directional hypothesis discussed in relation to the results from Experiment 12. Within the framework of this hypothesis, reaches that require correction towards an ipsilesional target would produce more corrections than for targets requiring a contralesional movement, as the coupling of the hemifield and the hand within the hemisphere would be advantageous for same-sided detection and control.

What is interesting to note however, is that ML's correction latencies were within the normal range, yet she was significantly slower than controls in the perceptual discrimination task. The opposite was true for IG, on the same set of tasks, as she performed within the normal limits on the perceptual task in mid fixation, but was unable to make corrections towards the targets she was able to attentionally locate. This would suggest that the mechanisms involved in attentional and visuomotor control problems in optic ataxia could potentially arise from damage to independent mechanisms (Striemer et al., 2009).

General Discussion

Section four set out to address the neurological aspects of the autopilot system. The neurological aspects most commonly investigated with regard to the automatic pilot include the differences between information that is selected-for-perception and information that is selected-for-action via the two distinct pathways in the brain. Experiments 10-14 provide further support for the role of the dorsal stream in the production of online corrections, and Experiment 9 considers the differences in the specialisation of the dorsal stream located within each hemisphere.

The findings of Experiment 9 corroborate with the findings of other experiments presented in this thesis, and provide support for a specialised role for the left hemisphere in the execution of accurate aiming movements. The bias that was present in the correction efficiency for targets presented on the right extends beyond a biomechanical explanation for the relative ease of ipsilateral movements compared to contralateral movements, as the reverse was not true of the left-handed participants. Independent of handedness, the right hand produced the more efficient corrections, out-performing the left hand on all of the measured dependent variables, suggesting a specialisation within the left hemisphere for this type of task.

The distinction in the processing capabilities of the two hemispheres has been well established and the specialisation of the left hemisphere/right hand system for controlling the sequential aspects of the organisation of complex motor movements has been evidenced many times in the literature (Boulinguez et al., 2001; Elliott & Chua 1996; Fisk & Goodale, 1985; Gonzalez et al., 2006; Goodale, 1990; Milner & Goodale, 1995). Experiment 9 adds further support to this body of work, providing a thorough assessment of the lateral differences in the production of online corrections in a double-step task, which occur independent

of handedness. The findings pose questions about the additive influences of enhanced detection of the target and control of the acting hand within the same specialised hemisphere, and how the direct link of communication between the two contributes to the observed right hand advantage.

This advantage is not evident in the performance of the participants with optic ataxia, and in IG and ML there appears to a dissociation between the speed at which the target location is detected and the speed at which a correction is initiated to the new location. IG performed within the normal limits in the mid fixation condition of the perceptual task, but was unable to produce fast corrections to these same locations. ML, on the other hand, was significantly slower than controls to react to the perturbed target in the perceptual task, but was within the normal limits for the corrections she produced in terms of latency.

This suggests that IG's inability to produce corrections was not due to a secondary attentional deficit, and also that the processes required for a button press response to a conscious perceptual detection are rather different from those involved in the spatial updating of the trajectory during an ongoing movement (Striemer et al., 2009). This distinction can be understood within the framework of the dual-visual streams model (Goodale & Milner, 1992), yet the relationship between misreaching and online correction, both dorsal stream processes, is less clear.

The examples of impaired obstacle avoidance in MH (Rice et al., 2003) and IG (Schindler et al., 2004) published in the literature demonstrated a matching between these difficulties and the impairments in misreaching, Furthermore, Blangero et al. (2008) had suggested that CF's hand and field effect in his reaching performance was mirrored in his pattern of performance for online correction. The reaching deficits, for these patients, were almost exclusively produced in extrafoveal space and thus it was hypothesised that the defict in

online correction could be explained by the same inability to use extrafoveal information to guide immediate action.

Experiments 10 and 11 were inconclusive with regard to this hypothesis, as MH struggled to produce any corrections in free vision in his non-ataxic hemifield, much less in the lateral fixation conditions. The conclusion of these experiments was that although the task had been designed to allow the comparison of MH's reaching and correction performance in ataxic and non-ataxic regions of space, no corrections were produced, and the task may have revealed asymmetrical bilateral symptoms in MH, which contributed to his performance on our sensitive task.

The findings from the MH study and the recruitment of bilateral optic ataxic IG meant that in order for the target to be perturbed to a non-ataxic region of the visual field, the target needed to be perturbed to central vision, and therefore the point of fixation. It was predicted that bilateral optic ataxic patient IG would not make fast corrections for targets jumped to extrafoveal locations, but would do so for targets jumped to her point of fixation. IG's reaching to static targets confirmed the sensitivity of her misreaching to retinal eccentricity, in that her performance deteriorated for extrafoveal targets in the lateral fixation conditions, in comparison with foveal targets in the mid fixation condition. However, her online correction abilities did not similarly depend on the location to which the target was jumped. Fast corrections were universally absent for IG and, most critically, there was no benefit when the target jumped to her point of fixation. This refutes the extrafoveal hypothesis, and implies that the location to which the movement is initially directed is important in determining the online correction deficit in optic ataxia.

The importance of the initial target location was corroborated in Experiment 14, with ML, following an inconclusive set of results from CF in Experiment 13. ML's pattern of corrections did not match her pattern of misreaching and in the

double-step task the direction of the target jump appeared to be an influencing factor in the efficiency of the corrections produced. The leftwards jump in the mid fixation condition produced a very pronounced field effect, and produced poorer performance compared to the right jump in the left fixation condition, where the target was perturbed to fixation. ML's online corrections struggled in the right fixation condition, where all targets were presented within her ataxic hemifield, and thus, the left jump matters for ML, thus appearing to provide support for the directional hypothesis. Within the framework of this hypothesis, reaches that require correction towards an ipsilesional target would produce more corrections than for targets requiring a contralesional movement, as the coupling of the hemifield and the hand within the hemisphere would be advantageous for same-sided detection and control (Goodale, 1990), as suggested by the manual asymmetries demonstrated in Experiment 9.

Chapter Five:

General Discussion

This thesis set out to investigate cognitive, attentional and neurological aspects of the automatic pilot, in three series of related experiments, all employing variations on a simple double-step reaching task. The detailed discussion of findings, and relation to prior literature, has been made within each chapter. This short closing chapter will simply recap the main findings, and proposed mechanisms to account for the results, briefly discuss limitations and suggest areas for future research.

Experiments 1-4: Cognitive aspects of the automatic pilot

Experiments 1-4 investigated how strongly automatic reach corrections are, by manipulating the influence of conscious intention and cognitive load. Conscious intention was manipulated via the introduction of a new instruction, the NOGO task, in which participants were required to continue to point to the original location of the target in response to the target jump. A common misconception in the literature about responses in the STOP condition being disallowed and still occurring was identified and addressed by the implementation of the NOGO instruction, and the ability to override the automatic compulsion to correct towards the new target location was reported, and has since been replicated by other groups (Cameron et al., 2009; Striemer et al, 2010).

The additional requirement of a concurrent auditory task disrupted voluntary inhibition of the automatic pilot, whilst leaving the voluntary enhancement

unaffected, suggesting that the automatic pilot is at most *weakly* automatic. The natural state of the online correction system does seem to be to follow the target to some extent, as reflected in the STOP performance, with the system reverting to the more reflexive corrective response when under heavy cognitive load.

The findings from all of the experiments reported in this chapter suggest that the role of cognition appears central to the successful performance in the double-step task, with the attentional set, as determined by the task instructions, integral to the pointing behaviour produced. These findings refute the concept of automaticity in reference to modularity (Fodor, 1983). The evidence demonstrates that the automatic pilot *is* sensitive to central cognitive goals, and that the system output is not autonomous or informationally encapsulated. The evidence from the case studies in Chapter 4 promotes the understanding that the automatic pilot is associated with a specific, localised neural structure, but that this structure interconnects with the inferotemporal cortex (Ungerleider & Mishkin, 1982) which allows cross-talk between the dorsal and ventral systems.

Experiments 5 – 8: Attentional aspects of the automatic pilot

Experiments 5 - 8 explored the properties of the visual target displacement that drive the automatic-pilot response in a double-step reaching task. These experiments demonstrated that correction efficiency is lawfully related to jump salience, and that the onset of the new target location drives correction responses more powerfully than the offset of the original target. The maximal correction rates, however, were obtained from a simultaneous onset and offset, in which the two components of the target jump are synergistic. It is suggested that this reflects the contribution of an apparent motion signal which strongly drives the automatic pilot system, but also allies with factors known to be

important in the selection of information for perception. Notably, bottom up and stimulus driven behaviour observed in both the perceptual and action paradigms 'turns out to be subtly influenced by top-down goals' (Pashler, Johnston & Ruthruff, 2001, p. 637), with cognitive settings manipulating the capture of attention.

Experiment 9: Neurological aspects of the automatic pilot (handedness)

Experiment 9 examined an asymmetry in correction efficiency, favouring rightward over leftward target jumps, evident throughout the earlier experiments, providing support for a specialised role for the left hemisphere in the execution of accurate aiming movements. The findings of Experiment 9 corroborate the findings of the other experiments presented in this thesis, and provide support for a specialised role for the left hemisphere in the execution of accurate aiming movements. The rightward bias cannot wholly be explained biomechanically, as the pattern did not simply reverse for the left-handed participants. Independent of handedness, the right hand produced the more efficient corrections, out-performing the left hand on all of the measured dependent variables, suggesting a specialisation within the left hemisphere for this type of behaviour.

Experiments 10 – 14: Neurological aspects of the automatic pilot (optic ataxia)

Finally, Experiments 10 - 14 considered whether the automatic pilot deficit in optic ataxia is simply a manifestation of the more general misreaching deficit. A series of single case studies eventually concluded that the misreaching deficit towards targets in extrafoveal locations could not account for the pattern of

deficits of online correction. MH was unable to successfully complete the task in either free vision (Experiment 10) or with lateral fixation (Experiment 11). There were no benefits for IG when the target was perturbed to her non-ataxic central vision, and she did not produce any fast corrections in any of the fixation conditions in Experiment 12. The findings from CF were inconclusive in determining the influence of T1 location rather than T2, but the recruitment of unilateral optic ataxic patient ML (who also had unilateral brain lesions) provided the opportunity to establish the influence of target jump direction and thus hemispheric specialisation for successful production of fast corrections. The inability to produce fast corrections is a specific functional consequence of dorsal stream damage (Gréa et al., 2002; Pisella et al., 2000), and the present findings suggest that the deficit is a directionally-specific one, suggesting that each hemisphere preferentially subserves online corrections towards the opposite side of space. This finding will need to be replicated in other unilateral optic ataxic participants, who have unilateral brain lesions.

Limitations, strengths and future directions

One inherent limitation of the set of studies presented in this thesis is the exclusive use of the double-step task. As explained in Chapter 1, there are many ways in which spatial errors can be artificially introduced into an ongoing trajectory in order to study the motor system's corrective response, for instance, by applying a force to the moving arm (e.g. Wolpert et al, 1995), or by using optically-displacing prisms to perturb vision of the target, so that the initial movement is inaccurate (e.g. Jakobson & Goodale, 1989). The double-step task induces a spatial error by changing the position of the target during the course of the reach. This is the most popular method used in the literature, and is most accommodating to adaptations. However, it is important to question the degree to which conclusions drawn from the double-step can be generalised to online correction behaviour more widely, or are task-specific.

This concern must particularly be acknowledged for the present form of double-step task, in which the target jump is made in free vision so that the participant is fully aware of it. This may model ecological situations of reaching for mobile targets, but might not be representative of online correction behaviour more generally. It is therefore important to acknowledge the influence that the choice of paradigm may have had upon the results and conclusions of the present experiments. For instance, it is simple to design a NOGO task within this framework, since it only requires the experimenter to ask the participant not to follow a target jump (but go to the original location). In fact, participants proved themselves well able to do this (Chapter 2), providing key evidence against strong automaticity of the automatic pilot. However, it is an open question whether participants would have been similarly able to suppress corrections to target jumps applied during saccadic suppression, which they did not consciously perceive, or in a task in which motor errors were induced by perturbation of reach programming (e.g. using optical prisms) or execution (e.g. by applying force to the limb). Similarly, the attentional influences upon correction efficiency described in Chapter 3 are very specific to the double-step task, and would have no equivalent in tasks where the motor error was not induced by a change in the target, so visual and non-visual factors related to the detection of motor error in hand position should also be carefully considered. Chapter 4 (neurological aspects) therefore has the same general limitation, and all the topics of the present thesis would be useful to explore in the context of alternative experimental models of online correction, in order to determine which conclusions relate specifically to target perturbation, and which to online correction more generally.

One aspect which must be acknowledged is the method by which rates of corrections and horizontal acceleration were calculated and analysed. As described in Experiment 1: Methods: Data processing and analysis, the correction rates were calculated on an individual basis for each participant from their unperturbed trial performance. The mean rates for each participant were

then analysed at each of the 10ms time bins, up to 350ms. This resulted in multiple ANOVAs being performed within each analysis, which could result in an inflated type 1 error rate. One way of reducing the number of levels in the time factor, would have been to start the analysis at 350ms and work backwards through the time bins, until there was no significant differences detected. This would have avoided multiple analyses on data collected towards the beginning of the movement, which as can be seen in Figure 3 (for example), would not warrant statistical investigation. However, the patterns of results in the Figures presented are very clear, and thus the statistical analysis reported in the thesis is acceptable. An alternative method of analysis conducted by Veerman et al. (2008) for horizontal acceleration involved using the difference from baseline to establish the additional velocity, and plotting the mean response for each participant. The latency of the correction was identified at the intercept with 0, and the slope of the plot indicated the intensity of the corrective movement.

Although the use of a single experimental paradigm is restricting in one sense, this limitation of the present work should not be overstated. Indeed, it is arguably a great strength of the present thesis that such a simple task design has served, with a range of minor variations, to illuminate such a range of issues in online control, and the use of a consistent task and analysis strategy has allowed for maximum comparability of the findings across studies. The double-step task has shown itself as sensitive to subtle variations in task instructions, stimulus conditions, manual asymmetries and neurological damage. This thesis presents robust findings that are evident in small sample sizes, with noticeable individual variability in performance (especially in the ability to follow the NOGO instruction in Experiments 1 and 2). Other studies have reported that individual variability is consistent across conditions (Veerman et al., 2008), yet this was not analysed in the thesis as the conditions were a between-subjects design for all experiments with the exception of Experiment 4.

Therefore, in addition to expanding the range of experimental models used to investigate online control, there is considerably more mileage in the double-step task itself. However, in taking this research programme forward, it will be important to consider more specific aspects of task design that might have important implications for experimental outcomes. Two key elements to be considered in future application of the double-step task are the number of potential target locations, and the clear difference in correction responses when using the two hands. In Experiments 1- 8, there was a predictable location of target perturbation, with only two potential locations, so a target on the left could only jump to the right and vice-versa. This design has been used in earlier studies (Pisella et al., 2000; Brenner & Smeets, 2004; Cressman et al., 2006) and may have enhanced performance in the GO condition (i.e. more corrections) and also in the NOGO condition (i.e. less corrections). It has now been demonstrated in a more recent study by Striemer et al. (2010), that the rates of suppressed corrections were much lower, when the target jump location was less predictable. Spatial predictability could aid the suppression of corrections by the need to inhibit only one location (although this is controlled for in Experiment 2), and as a consequence tasks such as ours would tend to overestimate how easily the automatic pilot can be disengaged. This overestimate would be relative to real-world situations in which target movements are unlikely to be so predictable.

Conclusion

The work of this thesis makes a significant contribution to the literature on the online control of manual aiming movements. It is a wide-ranging study of a number of aspects of a specific ability, which has proven in the previous literature to be fundamental to the understanding of brain function and functional anatomy. There are of course, theoretical and methodological limitations within the thesis, and issues that have not been addressed. Nonetheless, the conclusions drawn from this body of work significantly

advance our understanding of how the automatic – or the not so automatic – pilot operates to optimise our interactions with the world around us.

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